Optical cues and vision-based discrimination mechanisms underlying predatory versatility in jumping spiders (Araneæ: Salticidæ)

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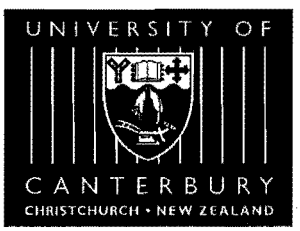

Duane Peter Harland
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Contents

Abstract

Acknowledgements

Chapter 1. Introduction

Chapter 2. Eight-legged cats and how they see

Chapter 3. The virtual lure presentation system

Chapter 4. Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals

Chapter 5. Prey classification by *Portia fimbriata*, a salticid spider that specializes at preying on other salticids: species that elicit cryptic stalking

Chapter 6. Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey

Chapter 7. Features of the anterio-median eyes of salticids that provide prey-specific cues to *Portia fimbriata*

Chapter 8. A knife in the back: discrimination of prey orientation and target choice by *Portia*

Chapter 9. Optical cues used by *Portia fimbriata* (Araneae: Salticidae) to target specific regions of spider prey

Chapter 10. Discussion

Appendix A. Eight-legged cats: A review on recent work on *Portia* and other jumping spiders (Araneae: Salticidae)

Appendix B. Reading a Spider's Mind

Abstract

Experimental studies of behaviour were carried out on jumping spiders (Salticidae), with particular attention given to araneophagic species in the genus *Portia*. *Portia fimbriata* was the primary species used in experiments. The objective of the research was to clarify mechanisms underlying visual perception, with this being part of a larger aim of understanding animal cognition. Literature on the structure and function of salticid eyes was reviewed in depth, with hypotheses and directions for future work highlighted. Distances at which salticid species distinguish prey insects from conspecific rivals was investigated using adult males of 37 salticid species. The discrimination distances recorded for most species imply higher levels of spatial acuity than has generally be appreciated for salticids. The longest discrimination distances found were for *Mogrus neglectus*, (max. 320 mm or 42 body lengths), with *Portia fimbriata* coming close (280 mm or 47 body lengths). *P. fimbriata* is unique among *Portia* spp.: all species of Portia prey routinely on other spiders (araneophagy), but *P. fimbriata* also has a specialised method of stalking and capturing other salticids. Optical cues by which *P. fimbriata* distinguishes salticid from non-salticid prey were investigated. *P. fimbriata*'s reactions to 114 salticid species were established. Except for *Myrmarachne* spp. (ant mimics), all salticids (both sympatric and allopatric species, species with aberrant body form and highly camouflaged species) triggered salticid-specific tactics by *P. fimbriata*. Experiments with odourless lures made from dead prey on which various combinations of features were altered imply that the large principal eyes of salticid prey provide optical cues that are critical for triggering *P. fimbriata*'s salticid-specific predatory tactics. Cues from the legs of prey salticids influence whether *P. fimbriata*'s stalks at all, but not whether salticid-specific tactics are adopted. Cues from the cephalothorax and abdomen also influenced

stalking tendency, but more weakly than cues from the legs. Using specially developed virtual 3D lures, presented to *P. fimbriata* on a projector screen, details concerning cues from the principal eyes of salticids were investigated. To be identified as a salticid, evidently there must be at least one principal eye on the face that is large and round. *P. fimbriata* distinguishes the orientation of salticid prey. A hypothetical model of how *P. fimbriata* distinguishes salticid orientation is discussed. That *Portia* spp. distinguishes the orientation of other non-salticid web-building spiders is also established in experiments where live prey are used. Using lures made from *Badumna longinquus*, a web-building spider, orientation-revealing optical cues were investigated. The research in this thesis suggests a framework for future studies.

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Last of all I thank the spiders (Portia and otherwise) who taught me the rewards to be gained from simply sitting patiently and watching.

Chapter 1. Introduction

Unique eyes, acute vision and complex behaviour are the distinctive features that separate the jumping spiders (family Salticidæ) from all other spider families. Of the salticids that are well studied to date, those with the highest optical spatial acuities and most complex behaviours are species of the genus *Portia* (Land 1985; Jackson & Pollard 1996). This genus of salticids is the subject of this thesis.

Most salticids eat insects captured in the open without using a web, but *Portia* is an oddball that routinely enters the webs of other spiders to catch and eat the resident (Jackson & Blest 1982). Hunting in the prey spider's own web is dangerous, but *Portia* avoids becoming its intended dinner's own dinner by using complex, flexible behaviour to deceive and manipulate its victim. The web spiders on which *Portia* preys have poor eyesight (Land 1985). They perceive the world around them primarily by interpreting web signals (Witt 1975). Web signals are the tension, movement and vibration patterns transmitted across the silk comprising the web, and the spider's web can be envisaged as not only a snare for catching prey but also a component of the web spider's sensory apparatus. *Portia*'s success at araneophagy depends largely on being able to orchestrate the pattern of web signals received by the resident spider, a predatory tactic we call 'aggressive mimicry'. Using any combinations of its eight legs and two palps, *Portia* can produce virtually an unlimited array of web signals to control the behaviour of the resident spider prior to the predatory attack (Jackson & Wilcox 1998).

Portia's different prey spiders tend to be responsive to different signals, but *Portia* finds the appropriate signals by using a dynamic blend of pre-programmed tactics and trial-

and-error derivation of signals (Jackson & Wilcox 1993a). Trial-and-error is based on *Portia* using feedback from the prey spider to adjust the characteristics of the signals. Such flexible problem solving is unexpected in a spider.

As another example of flexible problem solving, *Portia* routinely makes detours when it pursues prey (Jackson & Wilcox 1993b; Tarsitano & Jackson 1997). For instance, *Portia* may take a path to reach a particularly dangerous spider from behind. We know from experiments that many of *Portia*'s detours are planned ahead of time on the basis of preliminary visual assessment of the environment (Tarsitano & Andrews 1999).

The especially complex and flexible elements of behaviour of Portia's behaviour are reviewed in depth in the first half of Chapter 2. Problem solving by trial-and-error learning, and problem-solving by forward planning are behaviours that are usually referred to as 'cognitive' and tend to be associated with birds and mammals, much larger animals, that have vastly more neurons in their brain than does a spider. There would seem to be an elementary engineering problem working against complex behaviour in a spider. How can *Portia* (or any salticid) organise especially complex behaviour with a brain containing so few neurons?

The basic question is, 'how does Portia know when to do what.' My objective is to investigate some of the decision rules that underlie optical identification and vision-controlled behaviour in *Portia*. The framework in which this objective fits is the study of animal cognition. However, studying cognition in any animal is a less than straight-forward endeavour and a spider is a very different animal from animals in which animal cognition is typically investigated (e.g., mammals and birds). The research presented here represents a step toward studying cognition in *Portia*.

Cognition can be broken down into a number of stages (Dukas & Real 1993): reception; attention; representation; memory; problem solving; and in some cases, communication

and language. My investigations overlap several of these stages, but a vital first step would seem to be understanding of how sensory information is processed. To understand reception, we need to investigate the physical nature of the animal's sensory system. Besides clarifying the kinds of information to which the sensory system is adapted to pick up, we need an understanding of constraints on the system. In the second part of Chapter 2, there is a review of the structure and function of salticid eyes with special attention given to *Portia*. Chapter 4 is an experimental study, using behavioural techniques, showing that salticid eyes support extraordinary spatial acuity, evidently exceeding by a wide range anything that has been shown for any other animals in the same size range.

Representation refers to when an animal identifies objects and situations. Representation is a level of cognition that goes beyond reception. It can be envisioned as the animal taking the raw material from the senses (reception) and moulding it into something from which behavioural decisions can be made and problems can be solved. At the level of neurophysiology there may be no real distinction between reception, representation and other stages of cognition. All should be, in principle, reducible to specific sequences of nerve excitation. The advantage of the concept of cognitive stages is that it provides an intelligible way of breaking down a complex system into components that become more tractable. Studying cognition solely from the level of neurophysiology is unlikely ever to be sufficient.

The basic information that is used by *Portia* to decide when to do what is at the level of representation. With *Portia* my first aim has been to find out what is represented, and then move on to investigate how it is represented. A major goal in my research has been to develop new tools for investigating representation in *Portia* and other salticids. In Chapter 3 I describe and discuss new methods for investigating representation using virtual 3D lures, constructed using a computer and presented to Portia through a projection system onto a

small screen. Virtual lures provide a level of flexibility that goes beyond what is possible using traditional techniques (e.g., experimentation using lures made from live or dead animals), allowing us to ask questions about representation that were previously intractable.

Chapters 5-9 are experimental studies of specific aspects of representation. *Portia fimbriata* from Queensland, Australia, includes in its predatory strategy a tactic (cryptic stalking) enabling it to prey effectively on common sympatric salticids from other genera. Chapters 5-7 investigate the cues responsible for cryptic stalking.

Chapter 5 is a survey of *P. fimbriata*'s response to a wide range of salticids (from 114 species) of varied appearance. Information on what salticids elicit cryptic stalking and which salticids do not, suggests potential cues that influence Portia's decision to adopt cryptic stalking. Chapter 6 is an experimental investigation of the major hypotheses from Chapter 5. Physical lures provide evidence that the presence of large front eyes are critical cues that trigger cryptic stalking. Chapter 7 takes Chapter 6 further. Virtual 3D lures are used to investigate experimentally what features of the salticid's eyes act as cues for *P. fimbriata.*

Chapter 8 is an experimental investigation of whether *Portia* perceives the orientation of different types of prey. Chapter 9 takes Chapter 8 further by experimentally investigating what body parts of a web-building spider, *Badumna loningquus,* provide *P. fimbriata* with orientation cues.

In Chapter 10, an overview of the thesis is taken. Cognition as a framework for studying Portia is discussed. Directions for future directions are discussed.

A cut-down version of Chapter 2 has been published (Harland & Jackson 2000). This is provided here as an appendix (Appendix A), Chapter 4 has been published in the *Journal of Zoology* (*London*) (Harland et. al 1999), Chapter 5 has been submitted to the *Journal of Zoology* (*London*) and Chapter 6 has been submitted to the *Journal of Experimental Biology.*

These three Chapters are presented here as a reprint (Chapter 7) and as copies of the submitted manuscripts (Chapter 5 & 6).

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Chapter 2. Eight-legged cats and how they see

Introduction

When it comes to spiders, salticids are not easily mistaken for anything else. In English, the common name for salticids is 'jumping spiders' and many are indeed phenomenal leapers. However, jumping alone is not what distinguishes salticids from other spiders. Some spiders can jump, but salticids are special because they make accurate vision-guided leaps at their prey and other targets. What puts salticids in a group on their own is their unique, complex eyes and acute eyesight, not leaping prowess. No other spider has eyes like these and no other spider has such intricate vision-guided behaviour. Stare at a salticid and it will stare back with large anterior medial eyes that give it an almost catlike appearance. The feline analogy is more than superficial (Land 1974), and a better common name for salticids would probably be 'eight-legged cats'.

Like a cat, a salticid uses more than its eyesight. Chemoreception and other modalities also play a role. However, like a cat, and unlike any other spider, a salticid locates, tracks, stalks, chases down and leaps on active prey, with all phases of these predatory sequences being under optical control (Forster 1982). Using optical cues, salticids discriminate between mates and rivals, predators and prey, different types of prey, and features of non-living environment (Crane 1949; Drees 1952; Heil 1936; Jackson & Pollard 1996; Tarsitano & Jackson 1997; Chapters 4-9). No other spider can see this well. In fact, salticid eyes are in some ways more like a cat's than any other arthropod's.

Resemblance between cats and salticids may go beyond the eyes. Animal intelligence, animal cognition and related topics, although long neglected by scientists studying behaviour, are now being taken seriously (Gallistel 1992; Griffin 1984, 1998). For cats, especially big

cats such as lions, many scientists might be ready to concede that these topics are relevant, but cognition is not a conventional topic in spider studies. There may be compelling reasons for the traditional portrayal of spiders as simple, instinct-driven animals (Bristowe 1958; Savory 1928), and the very notion of discussing 'spider minds' might seem comical, if not scientifically disreputable.

This chapter is a review of recent work on salticids that challenges conventional wisdom. Of the salticids that are well studied to date, those with the highest optical spatial acuity (Williams & McIntyre 1980) and most complex behaviour (Jackson & Pollard 1996) are species in the genus *Portia* (Wanless 1978). This review will focus on these high achievers. The larger framework into which much of the work presented in this chapter and this thesis fits is an interest in animal perception and cognition. Trying to understand how *Portia* sees might be envisaged as a first step in trying to understand how *Portia* thinks.

Portia's predatory strategy

Most salticids prey primarily on insects caught by actively hunting instead of by building webs (Richman & Jackson 1992). This may not be surprising. Having keen eyesight, why should a salticid need a web? *Portia*, though, is an oddball, not only hunting out in the open but also building a prey-catching web. There is more. *Portia* invades the webs of other spiders where it feeds on the other spider's eggs, on insects ensnared in the other spider's web and on the other spider itself. On top of all this, *Portia* is unusual in appearance, in nature not really looking like a spider at all, or even an animal, but instead like detritus in a web (Jackson 1996; Jackson & Blest 1982a).

Hunting in another spider's web is dangerous and *Portia* has evolved complex, flexible behaviour to avoid becoming its intended dinner's dinner. Instead of simply stalking or

chasing down its victim, *Portia* generates aggressive-mimicry web signals (Tarsitano *et al.* in press). *Portia*'s preferred prey (Li *et al.* 1997), web-building spiders, have only rudimentary eyesight (Land 1985),and perceive the outside world primarily by interpreting web signals (Foelix 1996). Web signals are the tension and movement patterns conveyed through silk of the web, with the spider's web being almost literally a sense organ (Witt 1975).

Portia makes aggressive-mimicry signals by manipulating, plucking and slapping web silk with any one or any combination of its eight legs and two palps. Any appendage may adopt a great variety of different movement patterns, and movement patterns of any one appendage, however complex, can be combined with different movement patterns of any number of the other appendages. On top of all the signals made possible by moving legs and palps, *Portia* also makes signals by flicking its abdomen up and down, and abdomen movement can also be combined in various ways with the different patterns of appendage movement (Jackson and Blest 1982a; Jackson and Hallas 1986). The net effect is that *Portia* seems to have at its disposal virtually an unlimited array of different signals to use on the webs of other spiders (Jackson and Wilcox 1993a).

Ability to make many different kinds of signals is important for *Portia* because how *Portia*'s prey, another spider, interprets web signals tends to vary considerably from spider species to spider species, and with the sex, age, previous experience and feeding state of the spider. Yet *Portia* uses aggressive mimicry against, and catches, just about every kind of web-building spider imaginable, as long as it is in a size range of from about 1/10th to 2X *Portia*'s size (Jackson & Hallas 1986).

Ability to make so many different signals is one thing, but how does *Portia* derive from its enormous repertoire the appropriate signal for each of its many victims? Two basic ploys appear to be critical (Wilcox & Jackson 1998): 1) using specific pre-programmed prey-

specific signals when cues from some of its more common prey species are detected; and 2) flexible adjustment of signals in response to feedback from the victim (i.e., trial-and-error derivation of appropriate signals). The first ploy, using pre-programmed tactics, is consistent with the popular portrayal of spiders as animals governed by instinct, but trial and error is an example of problem-solving behaviour and less expected in a spider. Using trial and error, *Portia* figures out how to deceive its different victims.

How *Portia* uses the trial-and-error tactic may be most easily appreciated when *Portia* goes into the web of a species of web-building spider for which it does not have a pre-programmed tactic. After presenting the resident spider with a kaleidoscope of different web signals, *Portia* eventually chances upon a signal that elicits an appropriate response from the victim, whereupon *Portia* ceases to vary its signals and concentrates instead on producing this particular signal (i.e., the signal that worked; Jackson & Wilcox 1993a). If *Portia* is more powerful than its intended victim in the web, an appropriate response might be that the resident spider approaches as though *Portia* were a small ensnared insect, but the appropriate response is often be more subtle than this.

Aggressive mimicry for *Portia* is a dangerous predatory strategy. When facing a large and powerful spider in a web, it would be foolhardy for *Portia* simply to pretend to be prey and provoke a full-scale predatory attack. Instead, in these instances, *Portia* appears to strive for fine control over the victim's behaviour (Jackson & Wilcox 1998). This may be by making signals that draw the victim in slowly. Alternatively, signals may keep the victim calm while *Portia* moves in slowly for the kill, with the calming effect often being achieved by monotonous repetition of a habituating signal. Sometimes *Portia* appears to use trial and error to manoeuvre the prey spider into a particular orientation before attacking. Pholcids, for instance, are especially dangerous spiders with very long legs. Once a leg is contacted, pholcids

defend themselves and sometimes kill *Portia* (Jackson 1990, 1992a, b). The best way for *Portia* to catch a pholcid is to grab hold of its body without first hitting a leg. Using trial and error, *Portia* may coax the pholcid into a position from which a clear shot at the body is possible.

Even during encounters with spiders for which *Portia* has pre-programmed signals, trial and error may still be relevant, as the role of the pre-programmed signal appears often not to be simply to solve the problem of how to catch a particular spider but instead to get the predatory sequence off to a good start, after which *Portia* finishes the job by trial and error (Jackson & Wilcox 1998). The victim spider may, for instance, begin to approach slowly, then lose interest, become distracted, or begin approaching too fast. When, for any reason, pre-programmed signals stop working, *Portia* switches to trial and error.

Generating signals is not the only facet of *Portia*'s predatory strategy that is employed to hunt spiders in their own webs. Hunting in webs involves a complex interplay of tactics, driven primarily by visual and tactile feedback. Another common tactic adopted while stalking web-building spiders is the use of opportunistic smokescreens (Wilcox et al. 1996). Even a light breeze can cause large-scale displacement of the silk which tends to mask out the small signals made by *Portia* as it walks. *Portia* uses background noise from wind, from the struggles of insects on the web and even movement made by the web-spider itself to time its advances towards the prey. *Portia* is remarkably discriminating in its use of the opportunistic smokescreen tactic, using it when stalking a spider in a web, but not when stalking the web-building spider's own prey (ensnared insects) or its eggsacs (Wilcox et al. 1996).

Flexibility is a factor in *Portia*'s predatory strategy not only when invading webs, but also during navigation, with detouring behaviour being the most extensively studied example of this (Tarsitano & Andrew 1999). *Portia* routinely reaches prey by taking indirect routes

(detours) when direct paths are unavailable (Tarsitano & Jackson 1993), including 'reverse-route detours' (i.e., detours that require movement initially away from prey) (Tarsitano & Jackson 1994,1997). In encounters with some of its prey, *Portia* takes detours by choice even when direct routes are available (Jackson & Wilcox 1993b). *Scytodes* sp., a spitting spider from the Philippines, is particularly dangerous, its preferred prey being salticids (Li & Jackson, unpubl.). Detours enable *Portia* to approach spitting spiders from the rear, the safer end (Jackson et. al. 1998).

That *Portia* makes deliberate detours which are planned ahead has been corroborated in laboratory experiments. For example, when allowed to choose between two routes on artificial vegetation in the laboratory, only one of which leads to a prey spider, *Portia* consistently takes the appropriate path even when this means initially going away from the prey, going to where the prey is temporarily out of view and going past where the inappropriate path begins (Tarsitano & Jackson 1997). Lions have been observed making comparable detours when hunting their prey (Schaller 1972), and the taking of detours by lions has also been interpreted as demonstrating planning ahead. Lions, however, are much bigger animals with much bigger brains, and they are mammals.

One reason why cognitive attributes such as problem solving and forward planning are unexpected in a spider is brain size. Despite evidence that salticids have comparatively larger brains than other spiders (Meyer *et al.* 1984), the salticid brain is still minute. Fitting comfortably on the head of a pin, a salticid brain seems to vanish into insignificance when compared to the much larger brains of mammals such as dolphins, chimpanzees, elephants and lions (i.e., the kinds of animals for which questions about intelligence are routinely raised). Common sense tells us that a complex computer needs a lot of components. Miniaturising a computer requires miniaturised components, but miniature animals, such as spiders, do not

have miniaturised neurons. As a rule, smaller animals simply have fewer neurons (Alloway 1972; Menzel *et al.* 1984), and an elementary engineering problem would seem to work against animals in the salticid's size range. With so few components, how can they orchestrate complex and flexible behaviour?

Tackling cognition in *Portia*

An underlying goal of this thesis is to gain a toehold on understanding how vision interrelates with cognition in *Portia* and other salticids. Vision seems to be the primary sensory input for these spiders, and sensory input is the logical starting point for investigating cognitive processes. An analogy might be instructive.

Cognitive processes might be likened to recipes, but with the final product being behaviour rather than a meal. Typically, recipes consist of a list of ingredients and a series of instructions that transform the ingredients into the finished product. *Portia*'s cognitive processes can be envisaged, more or less, as recipes that take sensory information as ingredients and produce, as finished products, what *Portia* does. Our task is to reverse-engineer (see Dennett, 1996) the recipe from the finished product, as though a chef might start by finding a cake and then try to derive a recipe for this end product. For this exceedingly difficult task, ascertaining the ingredient list would appear to be a logical starting point. Certainty may be unrealistic, but at least some educated guesses may be possible. For uncovering the sensory ingredients on which cognitive processes operate, we might start by investigating the environmental input that provides sensory cues. This is the rationale for Chapter 4 - 9 where optical cues governing *Portia*'s predatory decisions are considered. However, optical cues need to be appreciated in the context of the structure and function of salticid eyes, the primary sensory structures used by salticids to gather information.

Since scientific methods were first employed in the investigation of salticid behaviour, there has been a strong emphasis on spiders' sensory systems (Peckham & Peckham 1887; Heil 1936), and especially vision (Peckham & Peckham 1894; Homann 1928; Drees 1952; Land 1969b, 1971). Having already reviewed key parts of *Portia*'s behaviour, the remaining parts of this chapter provide a review of how salticid eyes function and the limitations these eyes may have. Particular attention will be given to *Portia*. For a review focussing more on the histology of salticid eyes see Blest (1987).

Salticid and mammalian eyes compared

All salticids have eight eyes (Fig. 1, 2A) spaced around the cephalothorax. Acting together, these eight eyes perform the same fundamental functions as do the two eyes of a hunting mammal such as a human or a cat. Motion is detected. Its source is located and oriented towards. Located objects can be tracked, and the target's identity, size, range, orientation and behaviour can be determined (Land 1974). Irrespective of whether we are concerned with a salticid hunting a fly or a cat hunting a bird, the basic kind of visual information required is the same. What is more, salticids, like ourselves or a cat, have camera-type eyes (Land 1985a), which are very different from the multifaceted compound eyes of insects. However, there are important differences in how mammalian and salticid camera eyes perform the same tasks.

In salticids, the six secondary eyes, spaced along the sides of the carapace (Fig. 1), undertake the tasks of detecting motion and enabling the salticid to orient towards a motion source. The principal eyes face forward and are larger than the secondary eyes. It is the principal eyes that provide detailed information about objects towards which the salticid is oriented (e.g., the object's shape, texture and colour). In mammals the tasks that salticids

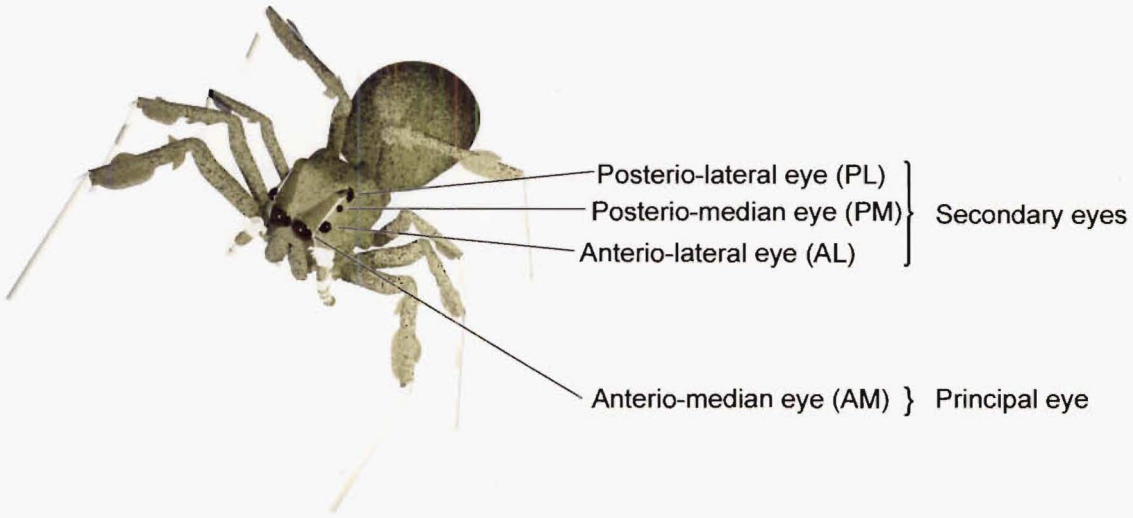


Fig. 1. Drawing of *Portia fimbriata* showing external arrangement of salticid eyes. Secondary eyes function in motion detection. Principal eyes function in high-acuity and colour vision.

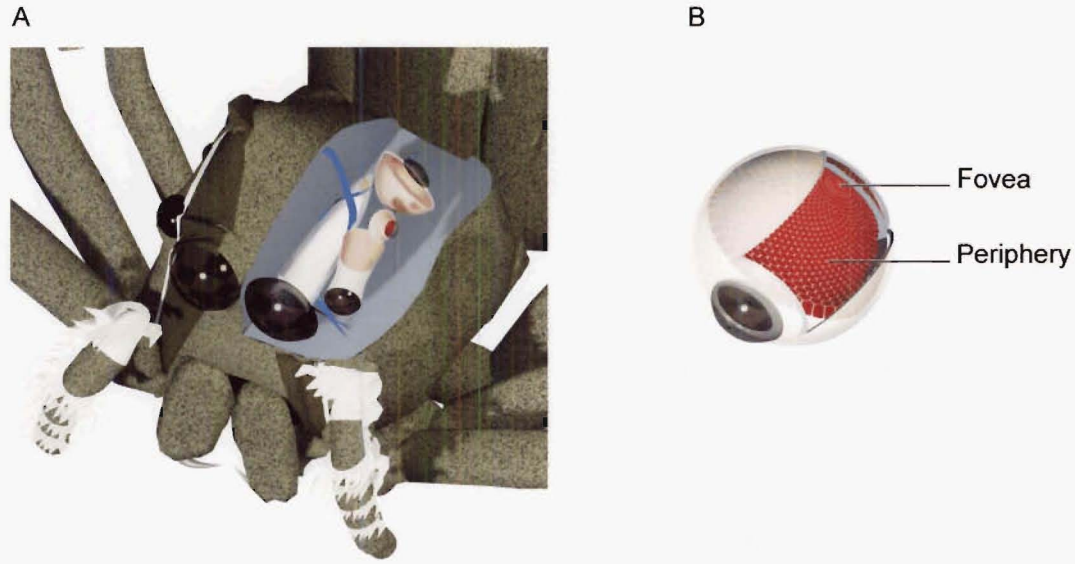


Fig. 2. Drawing of *Portia fimbriata* showing internal arrangement of salticid eyes. (A) Cut-open carapace showing long eye tube of principal (AM) eye and compact eye cups of secondary (Al, PM & PL) eyes. Structural tissue (e.g., eye tubes) shown in grey, retinae in red and muscles in blue (only the principal eye has muscles). (B) A mammalian-style spherical eye (at same scale and at same viewing angle as in A) that would be needed to incorporate the set of four (AM, AL, PM & PL) eyes represented in A into a single eye. To retain a focal length equivalent to that of an AM eye, the spherical eye's radius must be the same as the AM eye's depth. Even more space would be required for muscles (not shown). *P. fimbriata*'s cephalothorax would be filled with a single eye. A pair would simply not fit.

divide between the principal and secondary eyes are relegated to different types of cells on different parts of the retina. The mammalian retina is a single sheet of photo-receptor cells coating the inside back surface of the eye ball. The tasks of detecting motion and orienting the eye towards a motion source are mediated by the peripheral regions of each eye's retina, with detection of colour and shape being mediated by a central region called the fovea where the packing of receptors is especially tight.

The important ways in which the eyes of salticids differ from the eyes of mammals appear to arise primarily as evolutionary consequences of size constraints. For example, small size implies fewer cells. Transposing the equivalent of a spherical vertebrate eye into a salticid's body would not be a workable option (Land 1974). This is because optical performance in eyes is critically tied to the ratio between the lens' diameter (aperture) and its ability to magnify (focal length) (Land 1981). How much magnification (power) is provided by a lens determines how far behind the lens an image will form, and increasing the magnification means increasing the distance between lens and image. If we were to design spherical eyes with corneal lenses of equal aperture and the magnifying power (focal length) of the salticid principal eyes, the resulting pair of eyes would each have a diameter equal to the length of the principal eye. The extra volume required (~27 times more) would mean that each eye would, by itself, fill a typical salticid's entire cephalothorax (Fig. 2B). The salticid's solution to this size-constraint problem has been to divide visual tasks between two types of eyes, each type specialized for different tasks.

Secondary eyes

Both externally and internally, the six secondary eyes are smaller than the principal eyes (Fig. 1, 2A), but each secondary eye covers a much wider field of view than the principal eyes

(Fig. 3). The posterio-medial (PM) eyes of most salticids are regarded as vestigial because they have degenerate retinae incapable of movement detection (Eakin & Brandenburger 1971; Land 1985a) (Fig. 3a). That they may have functions other than movement detection is a possibility, but there have been no studies on this. Degenerate PM eyes are regarded as the derived condition and large functional PM eyes ancestral in salticids (Wanless 1984). Lyssomaninae and Spartaeinae are the taxonomically primitive salticid subfamilies, and many genera in these subfamilies have large PM eyes that function as movement detectors. *Portia*, for example, is a spartaeine genus and has functional PM eyes (Fig. 2a, 3b). In species with degenerate PM eyes, the fields of view of the remaining secondary eyes have apparently widened so that they encompass the fields that would be covered by functional PM eyes (Land 1985b).

Internally, each secondary eye has a regular mosaic of well separated receptors forming a bowl-like retina. The retina is made up primarily of three cell types, sensory cells, non-pigmented supportive cells and pigmented supportive cells (Eakin & Brandenburger 1971). Light is detected by proteins called rhodopsins, embedded in the plasma membranes of sensory cells. When an individual photons of light hits a rhodopsin molecule there is a probability that it will, by powering a chemical change in the protein, be absorbed. Chemical changes in rhodopsin by absorbing photons is how the light entering the retina is detected. As photon capture by individual rhodopsin molecules is relatively inefficient, large amounts of pigment must be placed in the light path. This is achieved by the membrane containing the rhodopsin being highly folded and situated in arrays of slender microvilli (rhabdomeres) held perpendicular to the surface of the retina and the incoming light. The part of the sensory cell that contains the rhabdomeres is called a rhabdom. Each receptor (independent functional unit

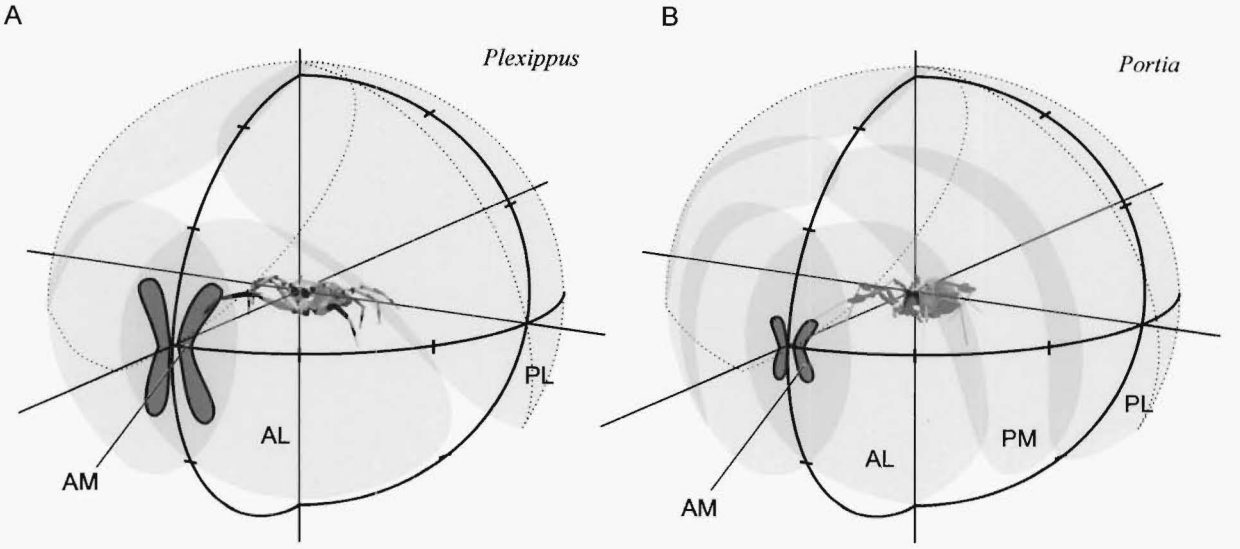


Fig. 3. Fields of view of eyes of (A) *Plexippus* sp., an advanced salticid (Salticinae) with vestigial posterio-median (PM) eyes, and of (B) *Portia fimbriata*, a spartaeine (primitive subfamily) salticid which has large functional PM eyes. Orthorgraphic viewpoint taken from 30° longitude and 15° latitude. Modified after Land (1985b). AM = Anterio-median eye. AL = Anterio-lateral eye. PM = Posterio-median eye. PL = Posterio-lateral eye.

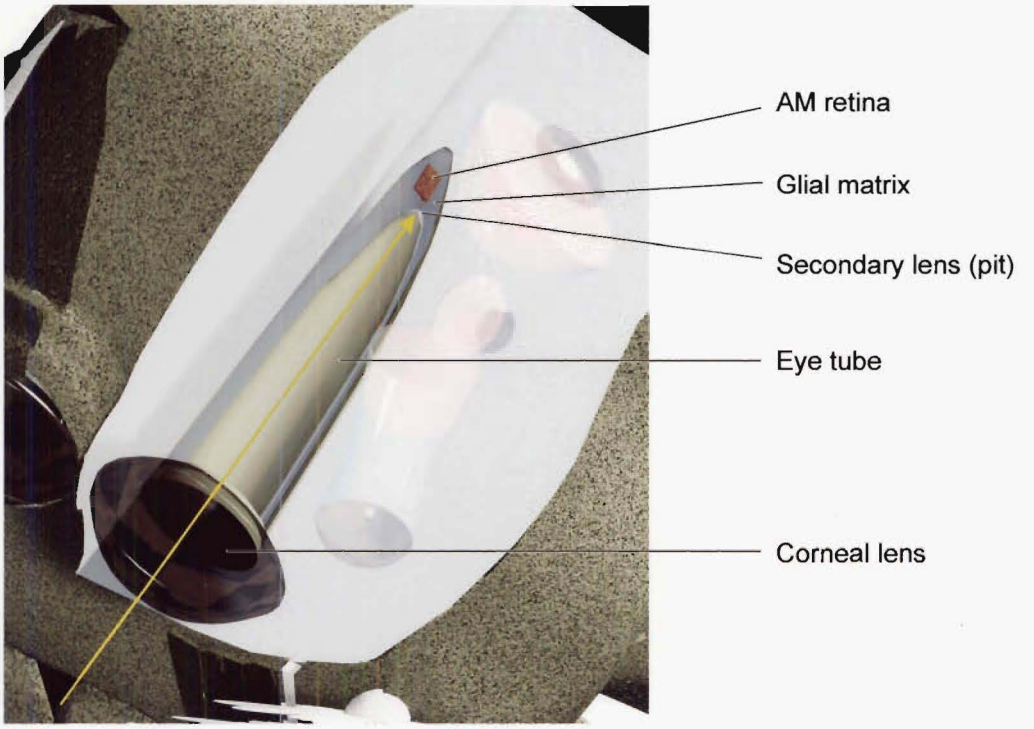


Fig. 4. Morphology of anterio-median (AM) eye of *Portia*. Light (yellow line) enters eye through the corneal lens and passes down the eye tube (cut longitudinally along its sagittal plane (dorso-ventral mid-line)) filled with glass cells (low optical density) before being magnified by the secondary lens (pit) formed by the interface with the glial matrix (high optical density). Images come into focus within the retina (red).

of reception) in the salticid secondary eye is made up of two contiguous rhabdoms surrounded by accessory cells (Blest 1985).

Focal lengths for secondary eyes tend to be small when compared with the higher acuity principal eyes, but small focal lengths help provide the secondary eyes with wide fields of view and large depths of field (i.e., distance range in front of eye over which an in-focus image is formed).

The secondary eyes' role as motion detectors is clearly suggested by the heavily pigmented accessory cells between receptors in the retina. Pigment protects each receptor from stray light penetrating the carapace or reflecting off other parts of the retina (Eakin & Brandenburger 1971; Blest 1985). Compared with receptors in the principal eyes, those of the secondary-eyes tend to be large in size. Being surrounded by supportive cells (Blest 1983), they are spaced widely apart.

Inter-receptor spacing and receptor width are critical factors defining the level of spatial detail an eye can resolve (i.e., the eye's spatial acuity). As the image falls upon the retina it is sampled by the receptors, each receptor sampling a specific small area. From each receptor the spider perceives a single 'dot' of light corresponding to the receptor's width. When receptors are wide, the sampled picture is made up of large dots and much of the fine detail of a scene remains unresolved. Gaps between receptors (as seen in the secondary eye retina) also influence acuity by corresponding to gaps in sampling. An eye's sampled spatial acuity as a 'visual angle' (defined as how far apart (in degrees) objects must be in a scene before they are seen as separate) is calculated from the inter-receptor spacing and the image's quality and spread (determined by the aperture and focal length of the lens). With visual angles varying between 0.4° and 2°, the spatial acuities of salticid secondary eyes tend to be comparable with those of the compound eyes of insects (Land 1985a, 1997).

Salticids detect movement when sequential changes in image intensity stimulate adjacent receptors in secondary eye retinae (Land 1971). A stimulus change between just two adjacent receptors is enough to elicit an orientation response. For example, a small insect walking along the ground to the side of a salticid might project an image on the PL retina that covers a single receptor. As the insect moves, its image will move from one receptor to the next on the PL retina, alerting the salticid to the presence of a moving object..

How readily a single receptor in the secondary-eye retinae can detect an object is strongly influenced the size of the image the object projects on the receptor. Size of the image depend critically on the object's size and its distance away. How strongly the object contrasts with the surrounding environment is also critical. For example, Land (1971) found that individual receptors from the PL eyes of *Metaphidippus aeneolus*, with receptive fields of 1°, responded to objects only if they projected an image wider than 0.4° on the retina. The probability of a response increased with the width and height of the stimulus, levelling out for stimuli larger than ~1.1°.

Any individual rhadopsin protein contained within an eye's rhabdoms is sensitive to a narrow band of wavelengths of light and different rhadopsin proteins can be sensitive to different regions of the spectrum (i.e., different wavelengths of light). An eye with receptors that are sensitive to different regions of the spectrum can be used to discriminate between objects based on the proportions of the different wavelengths reflected from them. That is, multiple types of receptors sensitive to different wavelengths of light forms the basis of colour vision.

Salticid secondary eyes are monochromatic (i.e., secondary eyes have only one type of rhadopsin in their receptors). In general terms this means that they see only in 'black and white'. Secondary-eye rhadopsin has maximum sensitivity (i.e., absorbs light maximally) at

wavelength of 535 nm (Yamashita & Tateda 1976; Hardie & Duelli 1978). This is the green region of the spectrum. On either side of its peak, absorbence by the rhabdom falls rapidly away.

In practical terms, this means that a salticid can detect that an object moves most readily when the object reflects light in the green region of the spectrum much more strongly, or much less strongly than the object's surroundings (i.e., contrast). For example, for a salticid, a green dot moving on a black background provides a high level of contrast and is easily seen. Likewise, a black dot moving across a green background would be easily seen, but an orange dot moving on a black background may not be detected at all.

When a movement is detected, a salticid may respond by orienting toward the object that moved and by bringing its principal eyes to bear (i.e., fixating them) on the source of the movement. Information from the secondary eyes governs orienting, which appears to depend on translating the position of stimulation on one of the secondary-eye retinae into a particular number of steps by the legs, moving legs on opposite sides of the body in opposite directions. This stepping turns the salticid a specific angle left or right (Land 1972).

When discussing algorithms that control orientation by animals a distinction is commonly made between, closed loop and open loop (Mittelstaedt 1962; Land 1971). Closed-loop turns require that the animal receives visual feedback from its own movement (i.e., the animal continually monitors the object's position). For this, the movement source must remain visible throughout the execution of the turn. In contrast, an open-loop turn is not governed by feedback It works on a single instruction and not a loop. For example, movement detected 80° to the animal's left can be envisaged as initiating an open-loop algorithm that reads, "turn 80° to the left, then stop." A closed-loop algorithm, in contrast, can be envisaged as reading some-

thing like, "turn a little in the direction of the movement source; if the movement source is in front, stop; if not, repeat from the beginning."

Open loop (not using feedback) means that, if the movement source is removed during orientation, the animal will never the less be pointing towards the object's last position at the completion of turning. By facing movement sources with a single turn, salticids appear to rely primarily on an open-loop algorithm. However, turning is occasionally performed as a series of smaller turns, suggesting that a closed-loop algorithm may also be relevant under some poorly understood circumstances (Land 1971).

Controlling orienting toward moving objects is the best known but not the only role of the secondary eyes. The interplay of the size, velocity, and movement patterns of moving objects are probably important for cueing different types of response. For example, objects that loom up (i.e., suddenly get bigger) may trigger escape behaviour (Heil 1936), with the speed at which an object increases in size probably being a critical factor. Even with objects that do not loom up, the speed at which it is moving appears to have important influences on the salticid's behaviour. In an object is moving especially slowly (e.g., below about 1°/s for *M. aeneolus*), typically no response is provoked. Objects moving especially rapidly (e.g., above about 100°/s for *M. aeneolus*) tend to provoke either an escape response, if large, or chasing, if small (Heil 1936; Drees 1952; Land 1971; Forster 1985).

When an escape response is triggered the salticid may retreat by, for example, quickly hiding, making a wild leap then freezing or running away. When running away from a predator, salticids appear to use information from the PL eyes to keep a pursuer directly behind (Land 1971). When chasing, instead of being chased, salticids appear to use information from the AL eyes to keep prey directly in front (Drees 1952; Forster 1979). Otherwise little is

known about how decision are made concerning reactions to different categories of movement.

Range finding is the task of determining the distance between the observer and a specific object. For salticids, range finding is important during hunting, for example, when the salticid must judge the distance from which to leap on prey. The salticid's AL eyes have a forward-facing region of binocular overlap (Fig. 3), which also overlaps the fields of view of each principal eye (Land 1985b). Experiments in which various eyes were covered with wax or paint, suggest that the AL eye overlap, coupled with the AM-AL overlap, play an important role in range finding (Homann 1928; Heil 1936; Forster 1979). However, the specific contributions of each eye are poorly understood.

Having the range-finding function restricted to the region of overlap between the AL eye's fields of view may impose significant constraints. An object (e.g., an insect) out to the side may be detected by the secondary eyes, but evidently the object must be in front of the salticid before it can be examined by the AL and AM eyes, as steps toward determining the type of the object detected (e.g., prey, predator, mate or unimportant stimuli) or its range. Suppose that a large (e.g., 10° diameter) object is moving behind the salticid. From the salticid's perspective, this could be a small object moving close by (e.g., insect prey) or a large moving object (e.g., a predatory bird) that is farther away. By orienting, a salticid may draw unwanted attention to its position, possibly triggering an escape response by prey or, worse, triggering an attack by a foraging predator. Yet the salticid would appear to be in a bind because orienting seems to be a necessary preliminary to determining the object's identity.

Salticids appear to be more reluctant to make larger turns and more willing to make shorter turns. For example, Land (1971) showed experimentally that a moving object behind

M. aeneolus and *M. harfordi* (i.e., stimuli that would require large turns) was less likely to provoke an orientation response than the same moving object just to the side. Perhaps reluctance to make large turns is partly a risk-reduction bias, as large turns would be more likely to have adverse consequences (frightening away potential prey or attracting a predator).

Unlike the other secondary eyes, each AL eyes contains a forward facing high acuity foveal region (Eakin & Brandenburger 1971; Land 1974). The function of the AL fovea has not been studied, but perhaps it has a role in range finding, or it might in guide saccades by the principal eyes (see below). Still other roles of the secondary eyes may await discovery. These eyes are almost certainly doing considerably more than simply detecting movement.

Principal eyes

Whether for a salticid or a human, the consequence of orienting toward an object is the same. A specialized part of the visual system is brought to bear on an object of interest. When a salticid turns to face an object, it brings an image of the object onto the retinae of its large anterio-medial (AM) eyes (Fig. 1). The AM eyes can now provide information that is different, and more detailed, than that provided by the salticid's secondary eyes. As a rough approximation, the salticid's secondary eyes are functionally equivalent to the peripheral regions of the human retinae and the salticid's principal eyes are functionally equivalent to the human fovea. Using their AM eyes, salticids discriminate between at least five broad classes of objects: mates, rivals, prey, predators and unimportant objects (Homann 1928; Heil 1936; Crane 1949; Drees 1952; Forster 1979; 1982). Some of the most basic decisions made by salticids in their day-to-day lives depends on this information. Finer-grain information is also important in the day-to-day life of many salticids.

Guidance of complex behaviour typically relies on the AM eyes. For example, *Portia* plans and executes detours based primarily on perceiving optical features of its environment (Tarsitano & Andrew 1999) and *Portia*'s complex, flexible prey-capture tactics rely on optical cues for resolving the identity and behaviour of prey from a distance (Jackson & Wilcox 1993a; Wilcox et al. 1996; Jackson et al. 1998; Chapter 9). Being adapted for high acuity, the salticid AM eyes can resolve fine details of objects at considerable distances. For example, *Portia fimbriata* can discriminate between prey and conspecifics at distances up to 46 body lengths away (Jackson & Blest 1982b; Chapter 4) and discrimination between parts of the environment used in navigation (e.g., detouring) can be made at even longer distances (e.g., from ~85 body lengths away; see Tarsitano & Jackson 1997).

Like the central foveal regions of our own retinae, the salticid AM eye retinae are adapted to receive the highest quality images possible and ascertain from these images information about shape, texture, and colour. Despite being used for many of the same tasks as the foveal regions of our own eyes, salticid AM eyes and human foveas have considerable structural differences. What we know about the structure of the principal eyes and the structure of its components can be illustrated by following the path taken by light entering into an eye (Fig. 4).

On the outside of the salticid's anterior carapace is the principal eye's large corneal lenses. The corneal lens is so named because, typical of terrestrial eyes (Land & Fernald 1992), the magnifying power of this lens comes primarily from light being bent by a cornea that is formed by a curved interface between the air and a hard surface. In salticids the cornea is formed by the carapace and it is both immobile (i.e., it can neither rotate nor move about in a socket as do vertebrate eyes) and non-malleable (i.e., it cannot change shape by bending). Behind the corneal surface of the corneal lens there is less power to bend incoming light, but

a gradient in lens density subtly redirects light rays in a way that corrects the spherical aberration from the cornea (Blest & Land 1977; Williams & McIntyre 1980; Forster 1985).

Despite their size, the combined fields of view provided by the AM eye's corneal lenses are eclipsed by those of the flanking AL eyes (Land 1969b; 1985b). This is because the focal length of the AM lens is greater than that of the AL. Having a greater focal length means greater magnification which in turn means that the image is spread out more and fine details are projected larger and can be more easily resolved. For salticids, having AM eyes that have a high magnification allows fine details of distant objects to be seen that would not be discernible to the secondary eyes. However, magnification comes at a price. Magnifying an image can be crudely envisaged as enlarging it by spreading the light more thinly over a larger area. This means that to magnify an image, yet retain the same brightness on all parts of it, more light is required. The only way to get more light is to make the lens wider. The other consequence of magnifying an image is that the more it is enlarged, the less of it will be in view. In short, by having a longer focal length the AM eyes have smaller fields of view than the secondary eyes yet require larger lenses to provide enough light to maintain an acceptable image quality for the magnified images they project.

Behind the AM corneal lens is a long, slightly tapering eye tube (Fig. 4). Transparent glass cells fill all except the rearmost part of the eye tube. After passing through the glass cells, light enters the matrix of cells supporting the retina (Eakin & Brandenburger 1971). Along the optical axis, the anterior interface of this supportive matrix forms a concave pit just in front of the retina (Fig. 4). This pit acts as a diverging lens that magnifies the image from the corneal lens (Fig. 5), boosting the eye's overall focal length. In *P. fimbriata*, the focal length of the corneal lens alone is 1237 μm. With the pit magnifying the image from the corneal lens, the eye acts as a telephoto lens system with a focal length of 1980 μm (Williams

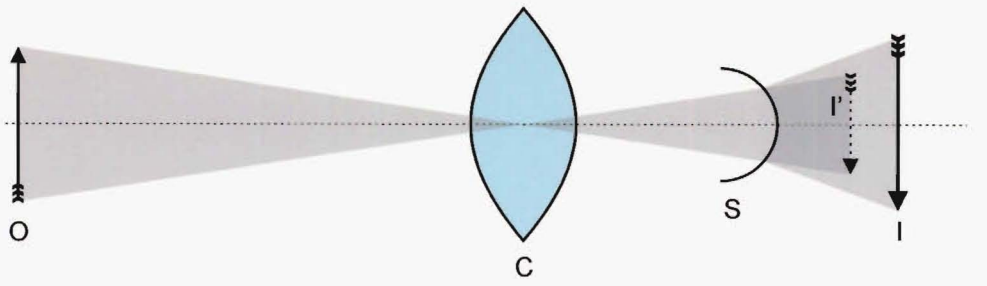


Fig. 5. Telephoto optics of salticid principal (AM) eye. Image (I) of object (O) is projected by corneal lens (C) onto retina after being magnified by secondary (diverging) lens (S) to make image of size I. I' shows what the approximate size and position of the image would be should the secondary lens be removed. Modified after Williams & McIntyre (1980).

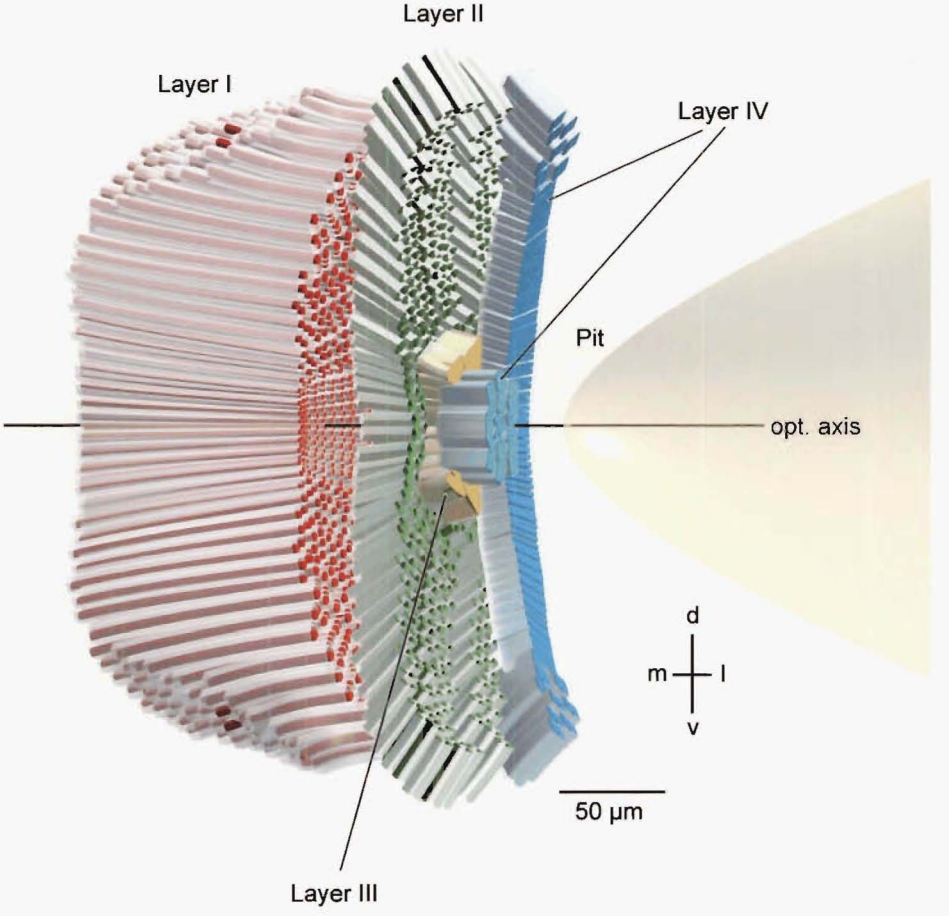


Fig. 6. Structurally complex retina of *Portia fimbriata*'s principal eye. Behind pit (secondary lens) are four layers of receptors (Layer I, II, III & IV) stacked along optical axis. Layers II, III, and IV contain more than one receptor type. Most receptors are short with somewhat irregular transverse cross-sectional profiles. Layer II type a and III type a receptors occluded by other layers in drawing. Layer I is highly ordered with well separated receptive segments. Interference between receptors reduced by this arrangement. Spatial acuities low as 2.4 min arc is supported by central fovea of Layer I. Orthographic view taken 55° from inner side of optical axis. Electron micrographs and structural descriptions from Williams & McIntyre (1980), Blest et al. (1981), Blest & Price (1984) and Blest (1987) used for constructing drawing. d: dorsal. m: medial. l: lateral. v: ventral. opt. axis: optical axis of the secondary lens.

& McIntyre 1980). Salticids are not alone in using a diverging lens as a space-saving method of increasing image magnification. The eyes of falconiform birds have foveal pits that operate as telephoto components (Snyder & Miller 1978) comparable to the pit in the salticid principal eye, providing these birds with the highest spatial acuities of any animal so far examined (up to 2.6 times greater than our own).

After being magnified by the secondary lens, the image formed by the AM-eye corneal lens is brought into focus on a complex retina. Unlike our own retina, the photo-receptors in the salticid AM retina are tiered into four distinct layers stacked along the light path (Fig. 6). To reach the rearmost layer of the retina, layer I, light first must pass progressively through layers IV, III, and II (Land 1969a; Eakin & Brandenburger 1971; Blest et al. 1981).

The tiered arrangement of the AM retina plays a critical role in colour vision. Light is split into a spectrum by the telephoto optics, with different wavelengths coming into focus at different distances behind the optics. This is known as chromatic aberration. Short wavelengths come into focus closer to the optics, in Layer IV, and longer wavelengths come into focus further from the optics, in Layer I. The eye's chromatic aberration is harnessed because the photo-receptors in the different layers each contain a different rhodopsin that is specifically sensitive to the wavelengths that come into focus on each layer (Fig. 7a) (Land 1969a; Blest et al. 1981).

Although receptors sensitive to wavelengths in the ultraviolet (UV), blue, green, and yellow parts of the spectrum have been found in the AM retinae of a few salticid species (DeVoe 1975; Yamashita & Tateda 1976), in only one species, *Plexippus validus* Urquhart, have the location of different receptors within the retina been determined (Blest et al. 1981). In *P. validus*, using marked cells, Blest et al. (1981) found that receptors in layer IV have peak absorbence in the ultraviolet part of the spectrum ($\lambda \sim 360$ nm) whereas receptors in layers I

and II have peak absorbence in the green ($\lambda \sim 520$ nm) part of the spectrum (Fig. 7b). Although Blest et al. (1981) did not succeed in sampling receptors from Layer III, optical calculations based on the position of the green and ultraviolet receptors suggested peak absorbence in the blue region of the spectrum would enable Layer III receptors to receive maximally sharp images. Wavelengths longer than green (e.g., red, $\lambda \sim 700$ nm) may also be absorbed at low efficiency by the green receptors in layers I and II (Peaslee & Wilson 1989), but there is no evidence that any salticid can discriminate long wavelengths (red) from other colours. For example, it would seem that a salticid cannot discriminate a red object from an otherwise identical dark green object.

Given the layered arrangement of the AM retina, it is tempting to assume that colour vision in salticids might work by simply combining the sampled images from the different layers (i.e., the image in green, blue, and UV) into a single colour picture. An analogy might be drawn to printing presses which make photographs by first laying down a single colour then overprinting the remaining colours one at a time until the full colour picture emerges. However, this cannot be the case because none of the receptor mosaics from any of the different layers match up and receptors in the different layers along any specific light path are of different sizes and shapes. This means that, for a salticid, deriving a colour picture can not be simply a matter of combining receptor for receptor what is sampled by the different layers.

Saying that salticids have colour vision is itself a complex issue because what it means to have colour vision is not straight forward. What we, as humans, mean by perceiving colours involves a myriad of factors. Some of these factors are at the level of the cells in the eye (e.g., three types of cones) and some are in how our brains interpret what they eyes provide (e.g., colour vision in the psychological sense). What colour vision means to a salticid is one of the bigger unresolved questions about salticid vision.

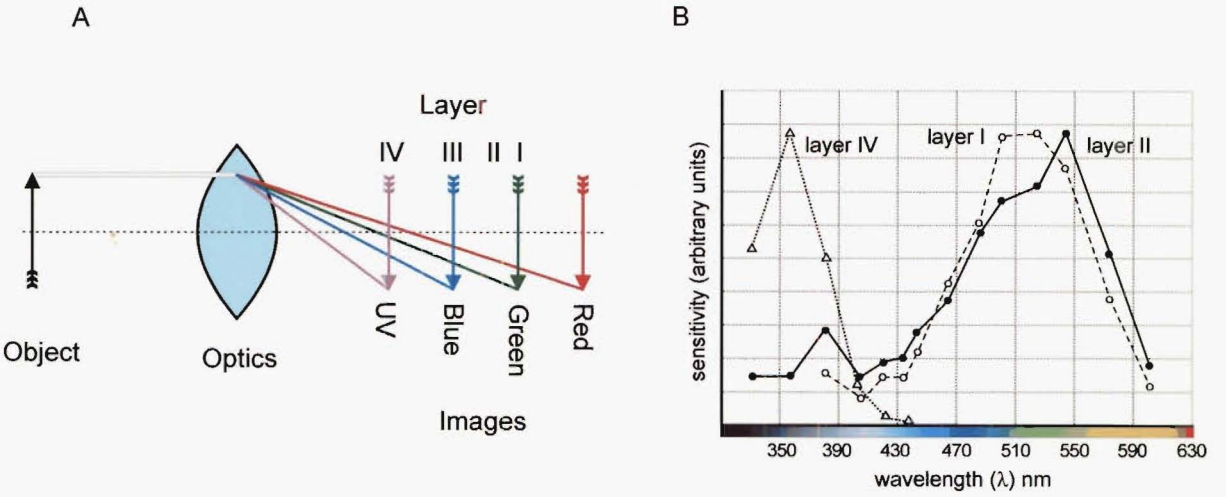
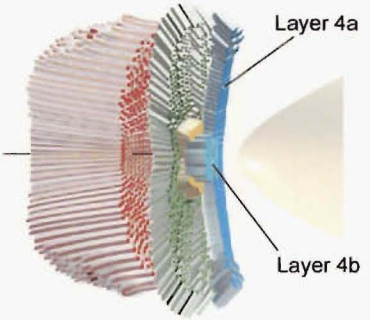


Figure 7. Hypothetical mechanism responsible for colour vision in salticids. (A) Chromatic aberration of the anterio-median (AM) eye optics is harnessed because the green, blue and UV components of an image come into focus on Layers I, III, and IV, respectively. (B) Spectral sensitivity of marked cells from layers IV, II and I within the AM eye of *Plexippus validus* (after Blest et al. 1981).



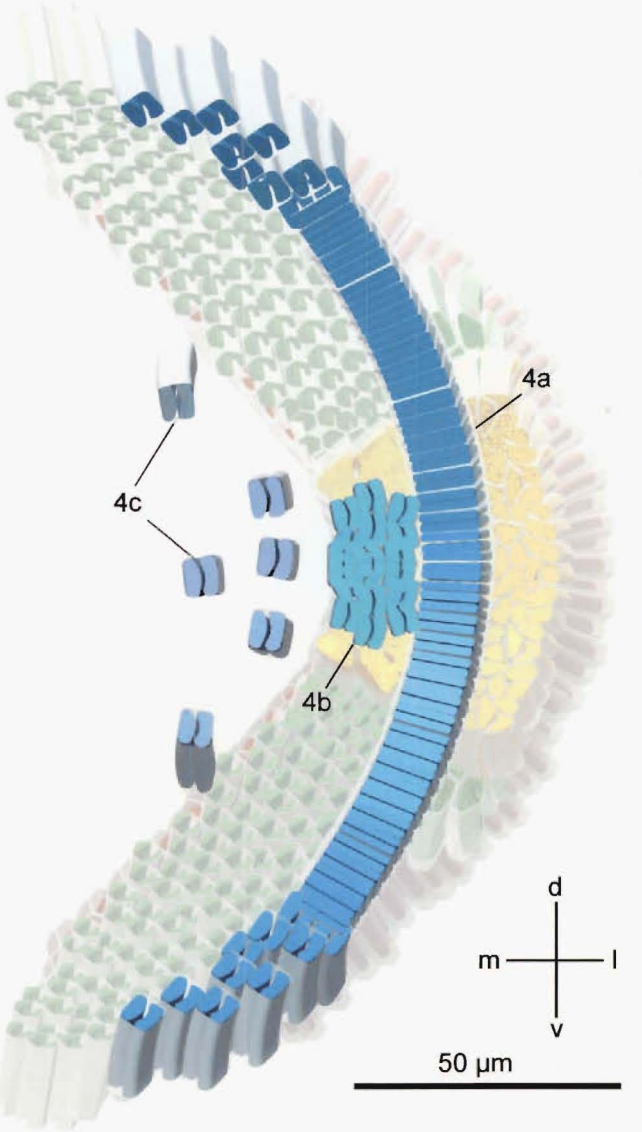


Fig. 8. *Portia fimbriata*'s principal eye retina showing Layer IV (blue) in detail. Position of Layer IV relative to other Layers within the retina shown at top (view angle, as Fig.6). Transverse profile of retina at right. Three types of receptors make up Layer IV. Type 4a receptors form well organised vertical strip that may act as a simple line detector, may be used to analyse the polarization of UV light or both. Type 4b receptors form poorly organized central patch. Type 4c receptors scattered to side (their positions within the figure are highly approximate). No function has been hypothesised for type 4b and 4c receptors. p: posterior. a: anterior. m: medial. l: lateral. d: dorsal. v: ventral.

Structural differences between each of the layers suggests that individual layers have functions that go beyond colour vision. Resolving fine details from a scene appears to be the primary function of Layer I because of this layer's fine grain. Layers II, III, and IV are coarse grain because they have large receptors and, compared with Layer I, poor sampling quality. The poor sampling quality of Layers II - IV may be necessary in order for Layer I to receive a good quality image (Williams & McIntyre 1980; Blest et al. 1981). An image will be degraded as light passes successively through Layers IV, III and II. Inter-receptor spacing and the way in which receptors are arranged in Layers II, III and IV diminish the spatial acuity of these layers' own receptor mosaics, but facilitate passage with minimal degradation of the image to Layer I. That is, the price for the back-most layer supporting high spatial acuity may have been poor acuity for the forward three layers.

Layer IV is the first layer encountered when we follow the path of light passing down the middle of the AM retina (Fig. 6). This layer has the poorest spatial acuity, but the most complex topography (Fig. 8) (Land 1969a; Eakin & Brandenburger 1971; Blest et al. 1981; Blest & Price 1984). A well-organized vertical strip of receptors lies along the outer side of the AM retina (4a), but the mosaic in the middle of the retina (4b) is especially poorly organized. Poorly organized regions also lie scattered towards the periphery (4c). The kinds of information the unusual arrangement of receptors in Layer IV might provide is unclear. It has been suggested that region 4a might support analysis of the plane in which ultraviolet light entering the eye is polarized (Land 1969a; Eakin & Brandenburger 1971). In other arthropods (von Frisch 1949; Brines & Gould 1982; Fent 1986), polarization detectors for UV light are known to serve as what might be called a 'sky compass', analysing the patterns of UV polarization seen in skylight during navigation. UV polarization detectors have been identified in the AM eyes of lycosids (Magni et al. 1964, 1965) and the secondary eyes of certain gna-

phosids and lamponids (Dacke et al. 1999), but no studies have been carried out on whether salticids detect the plane of UV-light polarization or use a UV sky compass.

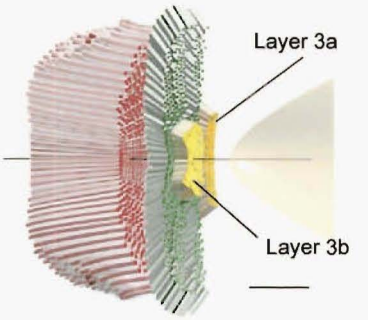
Directly behind the central region of Layer IV is Layer III (Fig. 9), the layer with the fewest receptors. This layer is confined to a patch that is roughly circular and situated in the middle of the retina (Land 1969a). Of the four layers, Layer III is functionally least well understood.

In *Portia*, Layer III is populated with large receptors and is especially irregularly arranged. Unlike in the secondary eye retina, receptors in the AM eye retina are not separated by pigment and for individual receptors to be independent their rhabdomeres must not touch. In Layer III, rhabdomeres from neighbouring rhabdoms are often contiguous severely reducing their effectiveness as independent receptors. This means that Layer III can support only very low spatial acuity. In the advanced salticids, Layer III is somewhat more organized than in spartaeines, but still not to an extent that can support more than modest acuity (Eakin & Brandenburger 1971).

In most salticids the receptor mosaic of Layer II has rhabdoms that are more regularly arranged and in which the rhabdomeres are less erratically contiguous than in Layer III. However, in the spartaeines this is not the case. For example, *Portia*'s Layer II mosaic (Fig. 10) is only slightly more organized than that of Layer III.

Rhabdoms in Layer II and III differ in appearance depending on whether they are derived from the outer side of the retina (2a & 3a) or from the inner side (2b & 3b), but no functional significance is known for how they differ.

In transverse section, Layers I and II have a laterally compressed strip of receptors with a slight bend in the middle. The result is a boomerang-shaped (Fig. 10, 11) receptor mosaic in each of these layers, Layer II's boomerang over Layer I's.



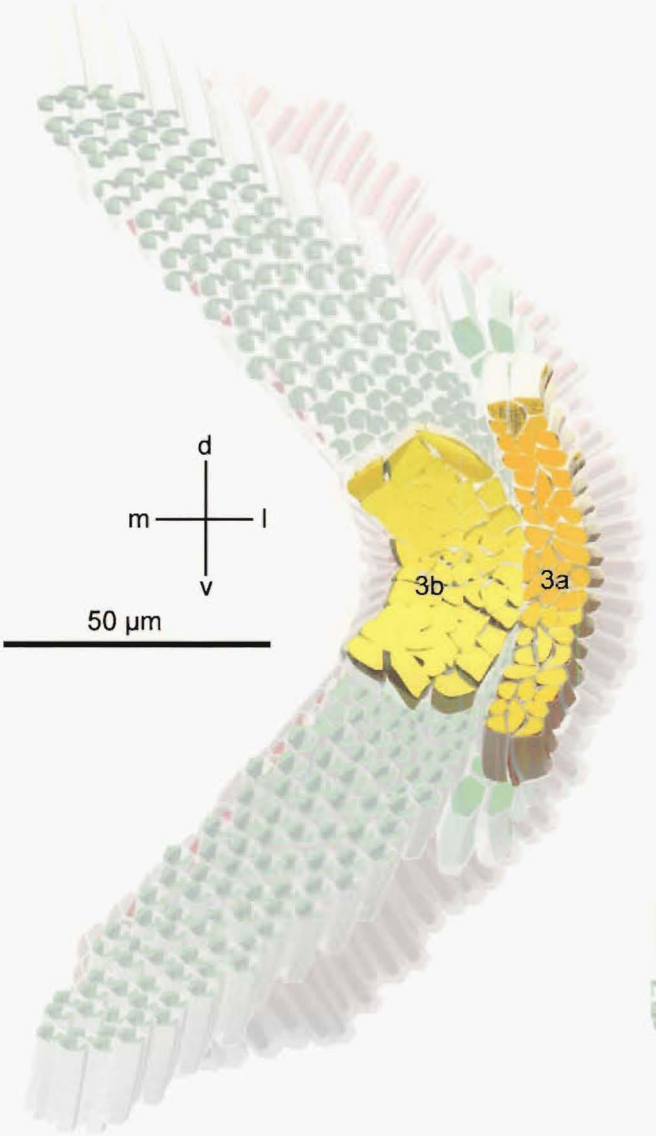


Fig. 9. *Portia fimbriata*'s principal eye retina showing Layer III (yellow–orange) in detail. Position of Layer III relative to other Layers of the retina at top (view angle as Fig.6). Transverse profile of retina on left. Two types of receptors make up Layer III, 3a and 3b receptors being large, short, irregularly disposed, and having rhabdomeres that are erratically contiguious. Layer III would receive an infocus image in blue. Quality of any image sampled by this layer would be extremely poor. p: posterior. a: anterior. m: medial. l: lateral. d: dorsal. v: ventral.

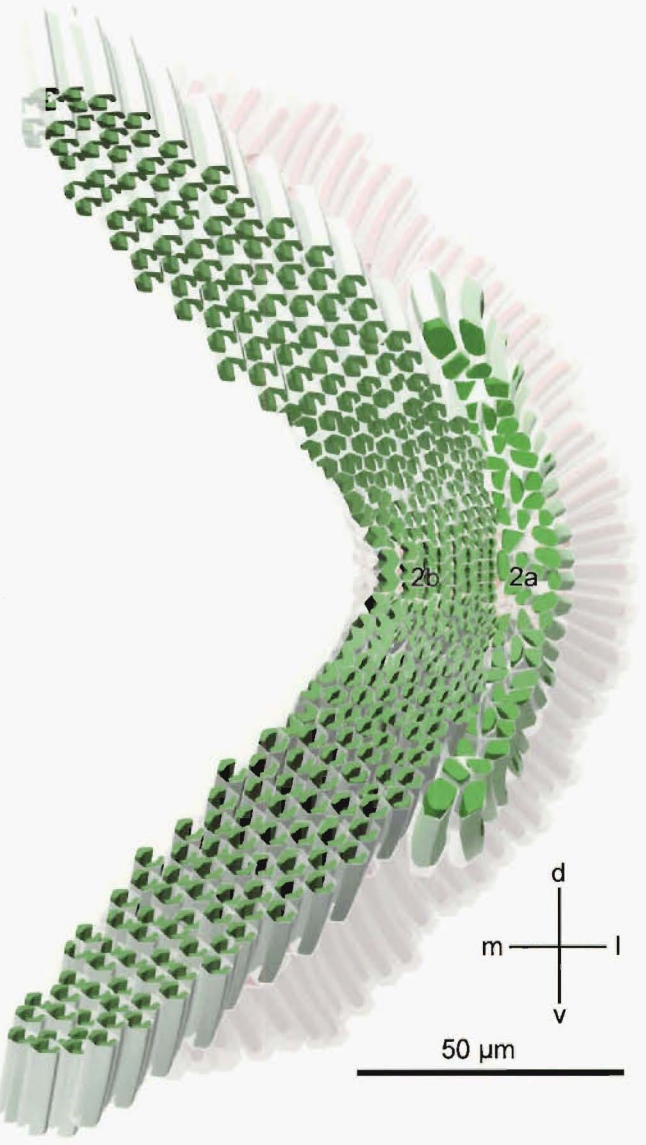
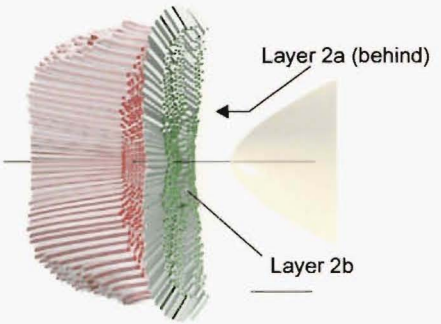


Fig. 10. *Portia fimbriata*'s principal eye retina showing Layer II (green) in detail. Position of Layer II relative to Layers I at bottom (view angle as Fig.6). Transverse profile of retina at right. Two types of receptors make up 'boomerang shaped' Layer II. At fovea of 2b, receptors have small inter-receptor angles (although not as small as in Layer I), but are arranged in a disorderly manner. Receptors increase in width towards the periphery of the boomerang arms and the mosaic becomes more regular. Compared with Layer I, receptors in Layer II are short. In *P. fimbriata* Layer II does not appear to be adapted for high acuity vision. p: posterior. a: anterior. m: medial. l: lateral. d: dorsal. v: ventral.



In *Portia,* receptor width, and therefore inter-receptor spacing, in layer II's central region (i.e., the region close to the optical axis) tends to be much greater than in the central region of Layer I. This means that the central region of Layer II has much lower spatial acuity. In both Layer I and II, receptor width and spacing tend to increase steadily towards the periphery until, at the ends of the boomerang's 'arms', inter-receptor spacing for Layer I and II are more or less equivalent (Fig. 10, 11).

Compared with their central regions, the peripheral regions of Layers I and II support only low spatial acuity. This may function to match the sampling quality (i.e., receptor grain) to the reduced image quality further from the optical axis. That image quality falls off rapidly away from the fovea may be because of the pit (Blest & Price 1984). Close to the optical axis, the pit lens magnifies without distortion, but further from the optical axis, the steep sides of the pit produce a more distorted image.

Because of its low acuity, the peripheral retina may play a different role in visual processing than the central region. One possibility is that the peripheral regions of Layer I and II may play a role in stimulating eye tube movements (see below) that line up the centre of the retina on moving stimuli (Blest & Price 1984).

The function of Layer II is especially unclear. No clear-cut role is suggested by the arrangement of the mosaic or the sensitivity of the receptors. The receptors in both Layers II and I have almost identical absorbence spectra (Fig. 7b) (i.e., they are sensitive to the same colour) (Blest et al. 1981). This means that either Layer I or Layer II would be redundant as parts of the colour vision mechanism. Shape perception seems unlikely because Layer II receives an out-of-focus image whenever Layer I receives one that is in focus. Perhaps Layer II functions in detecting light intensity (Blest et al. 1981), has a role in pattern recognition that

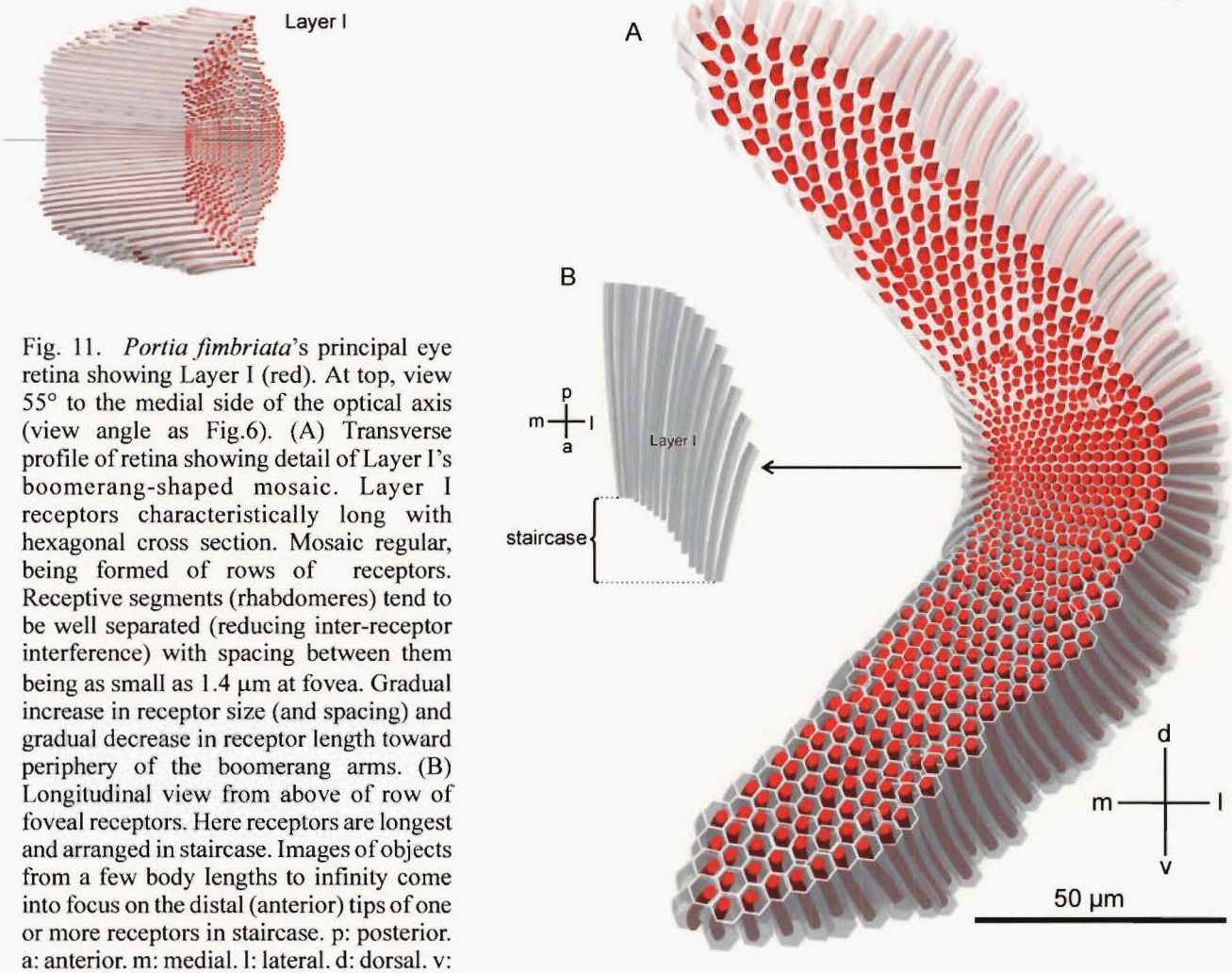


Fig. 11. *Portia fimbriata*'s principal eye retina showing Layer I (red). At top, view 55° to the medial side of the optical axis (view angle as Fig.6). (A) Transverse profile of retina showing detail of Layer I's boomerang-shaped mosaic. Layer I receptors characteristically long with hexagonal cross section. Mosaic regular, being formed of rows of receptors. Receptive segments (rhabdomeres) tend to be well separated (reducing inter-receptor interference) with spacing between them being as small as 1.4 µm at fovea. Gradual increase in receptor size (and spacing) and gradual decrease in receptor length toward periphery of the boomerang arms. (B) Longitudinal view from above of row of foveal receptors. Here receptors are longest and arranged in staircase. Images of objects from a few body lengths to infinity come into focus on the distal (anterior) tips of one or more receptors in staircase. p: posterior. a: anterior. m: medial. l: lateral. d: dorsal. v: ventral.

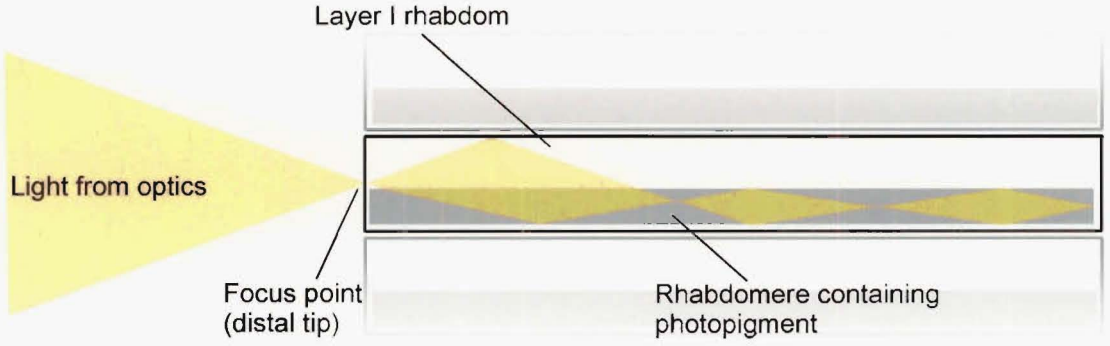


Fig. 12. Layer I receptor acting as a light guide. Light focussed on the rhabdom's anterior tip is trapped in the rhabdomere by internal reflection. Light passes back and forth through rhodopsin in rhabdomere, enhancing its probability of being absorbed (i.e., detected).

somehow complements the role of Layer I (Blest & Price 1984) or works with the secondary eyes to centre the AM retinae on moving objects.

For acute vision a fine, regular mosaic of receptors is expected. Of all the layers, only Layer I is organized in this way (Fig. 11). The internal structure of receptors, their width, length and spacing from other receptors are factors that combined define sampling performance. The most fundamental of these factors is the spacing between receptors. As inter-receptor spacing decreases (i.e., when the receptors are packed closer together), parts of an image that are closer together can be sampled, but there is a cost. Densely packed receptors must be narrow and to minimise spacing between rhabdoms, there is no space for opaque pigment between them. Having no shielding between receptors means that rhabdomeres from neighbouring receptors can potentially touch. Where rhabdomeres are contiguous they interfere with each other and reduce sampling quality. In the foveal region of Layer I the rhabdomeres, by being narrow and leaving gaps of cytoplasm between each, are arranged so that they are isolated from other rhabdomeres. Apart from not being shielded by pigment, being narrow means that less light from the image will enter the receptor. Less light and narrow rhabdomeres reduces considerably the probability of light being detected.

One way for narrow receptors to improve their detection efficiency is to have a longer rhabdomere. This increases the amount of rhodopsin that photons entering the rhabdomere travel through, increasing their probability of being detected. Compared with receptors from other layers, the receptors of Layer I are not only narrow but also long. Within Layer I the longest and most narrow receptors are in the fovea and the shortest and widest are at the ends of the boomerang's arms (Fig 6).

Being long is one way to improve the probability of photons being detected by a narrow receptor, but the foveal Layer I receptors have gone one better, and act as light guides.

Receptors in this but no other layer appear to function as light guides. Acting as a light guide improves sampling quality in two different ways. Firstly, instead of light coming into focus into the interior of receptors, it is instead comes into focus on their distal tips. This reduces the probability of a receptor's neighbours accidentally intercepting photons from that receptor's part of the image before they reach the focal point. This increases the sharpness of the sampled picture. Secondly, light guide receptors act as a miniature fibre-optic cables.

The material inside each rhabdomere is dense compared with the surrounding cytoplasm. When their incident angle is low, photons travelling through a transparent medium tend to be reflected rather than passing through (i.e., refracted) when they come to an interface with a less dense, but still transparent, medium. Inside the Layer I foveal receptors, as photons enter the rhabdomere they tend to become trapped because as they encounter the edge of the rhabdomere (assuming they are not absorbed by a rhodopsin protein first) they tend to be reflected back into the rhabdomere rather than passing out. However, unlike manmade fibre-optic cables that are used simply to convey light from one place to another, the rhabdomere also acts a detector. Photons are bounced back and forth through the rhodopsin increasing their probability of being absorbed (Fig. 12).

Layer I samples images at a high acuity by having receptors that are narrow and closely, but not too closely, spaced. In the fovea, neighbouring receptors have a centre-to-centre spacing as low as 1.4 μm. This appears to be optimal spacing. The telephoto optical system of the AM eye is precise enough to let the retina sample at this resolution, but quantum-level interference between adjacent receptors rules out having receptors closer together than this (Snyder 1972; Williams & McIntyre 1980; Blest & Price 1984; Land 1981). Light guides, rhodopsin and lenses are most easily understood when we think of light as a series of particles (i.e., photons), but light also has properties associated with waves. As the diameter

of rhabdomeres approaches the wavelength of light, waves travelling inside the rhabdomere interfere with one another. Interference patterns develop that cause the light distribution within the rhabdomere to become non-uniform and much of the light propagates down the sides of the rhabdomere. No amount of shielding, in the form of pigment or internal reflection, can prevent light leaving the rhabdomere due to this type of quantum interference. What is more, light that leaves the rhabdomere may be picked up by neighbouring receptors, reducing considerably the quality of the sampled image.

The high spatial acuity of Layer I, which depends on tight inter-receptor spacing and the spread and quality of the image from the telephoto system, can be expressed as a 'visual angle'. For example, the visual angle in *Portia*'s fovea is calculated by dividing receptor spacing of 1.4 μm by the telephoto optics' focal length of 1,980 μm. This computes out as 7.07×10^{4} radians, or 0.04° (2.4 min of arc) (Williams & McIntyre 1980). In practical terms, a visual angle of 2.4 arc min should allow *Portia*, from a distance of 200 mm away, to discriminate between objects spaced no more than 0.12 mm apart. Toward the periphery of Layer I receptor spacing increases, which means visual angle increases, and spatial acuity decreases.

These narrow receptors retain a workable level of sensitivity. They do this by virtue of being long and acting as light guides. The receptors can work as light guides only as long as the image from the telephoto optics is focussed on their distal tips. The human eye changes focal length (accommodates) to 'focus' on objects at different distances away. The salticid AM eye is a 'fixed lens' system, as it cannot accommodate. Objects at different distances in front of the eye will come into focus at different distances behind the AM lens system. For any specific receptor in Layer I, when a close object is in focus on the receptor's distal tip, more distant objects tend to be out of focus (and vice-versa). This potential problem for Layer

I is solved by having the receptors arranged in a spatial pattern that eliminates the need for accommodation.

Different parts of Layer I are positioned on a 'staircase' so that across the fovea their distal tips form stairs at different distances behind the AM lens system (Fig. 11b). Images of objects at different distances in front of the AM lens system come into focus on different stairs. The depth of the staircase (~20 μm) is sufficiently large for allowing an in-focus image to form on at least one of the stairs from a couple of body lengths away to infinity (Blest et al. 1981). Only Layer I has a staircase structure, inability to accommodate not posing a comparable problem for Layers IV, III and II, which have low acuity and do not function as light guides.

The telephoto optics, along with the unique structure of the AM retina, appears to provide solutions that allow a fixed-lens eye to provide both colour discrimination and high spatial acuity. However, one possible side-effect of how the AM eye is constructed may be that the field of view of the retina is highly limited. *Portia*'s Layer I fovea is only 15 receptors across, giving a field of view little more than 0.6° wide, much less than the ~30-40° provided by the corneal lenses. What is more, most objects examined by the eye will be out of focus at some part of the staircase, making the fovea's effective field of view even narrower. Yet the fovea, with a tiny field of view only a few receptors wide, supports the feats of visual discrimination that underlie much of *Portia*'s complex and flexible behaviour.

The AM eye is an active eye and this may be the key to understanding how the AM retina's narrow field of view works. Movement of the eye's field of view over a scene probably forms a critical part of perception. Using six muscles attached to the outside (Fig. 13), each AM eye tube, with the retina at its rear end, can be moved with three degrees of freedom: vertical, horizontal and rotation (Land 1969b). These are the same three degrees of freedom

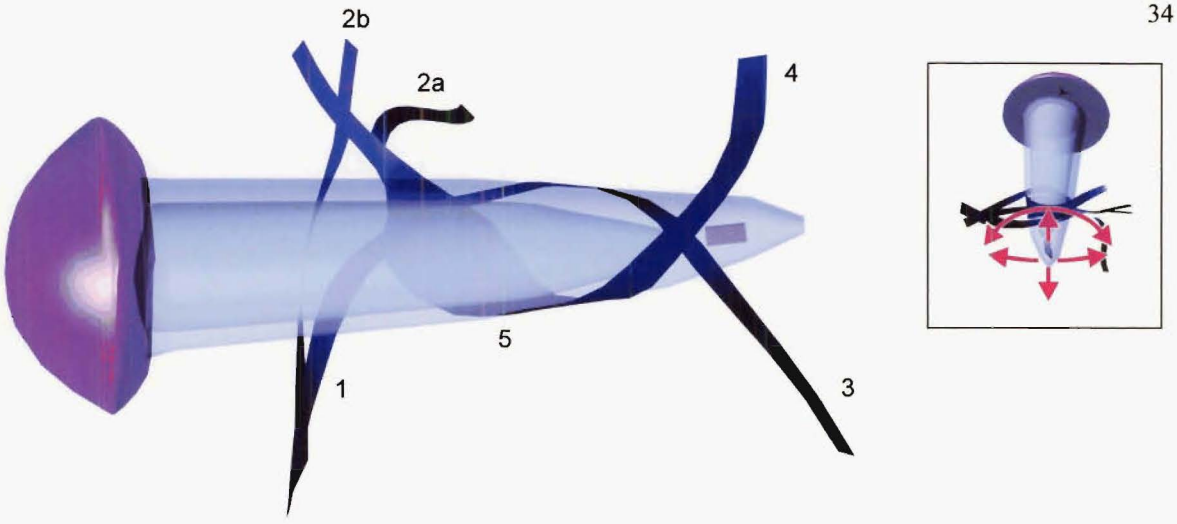


Fig. 13. Top view of *Portia fimbriata*'s left AM eye showing probable positions of eye muscles. Numbers after Land (1969b). Five muscle bands attached to eye tube allow retina to be moved (inset) in horizontal and vertical plane as well as rotated ~30° in either direction. Eye tube after Williams & McIntyre (1980). Muscles after Land (1969b). Although corneal lens is wider than eye tube (giving eye distinctive 'mushroom' shape), retina's field of view never blocked because retina, at any one time, samples only small part of corneal lens' field of view, and because retina can be moved to where images from sides of corneal lens are visible.

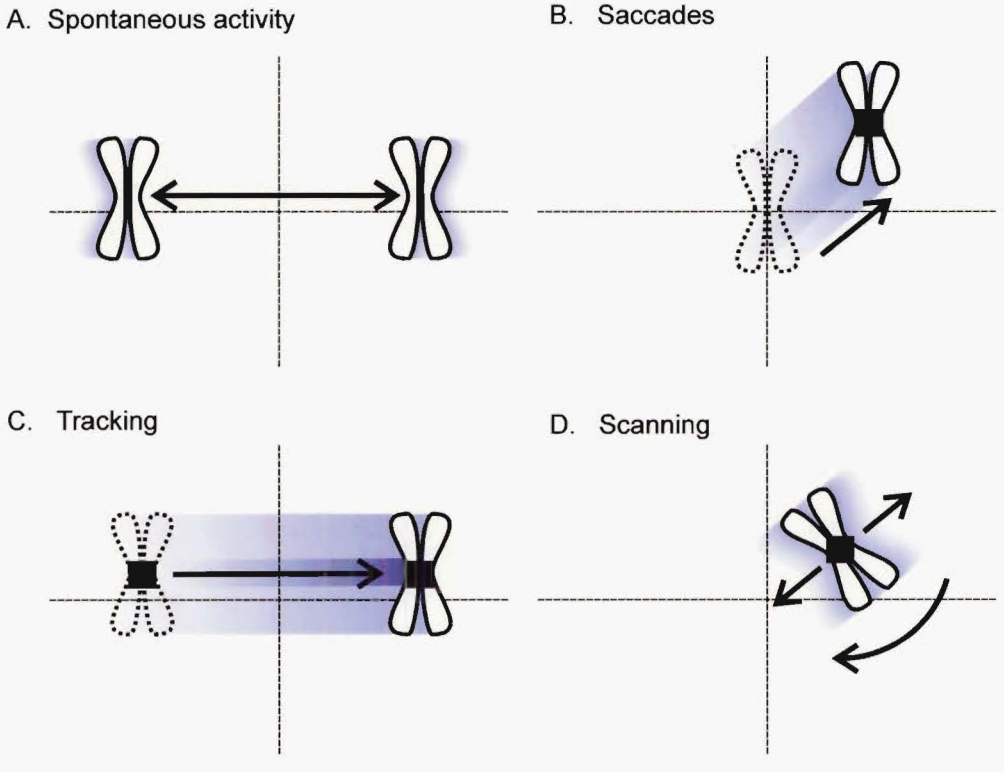


Fig. 14. Summary of four types of eye movement from the salticid anterio-median (AM) eyes (Land1969b). Fields of view from two boomerang-shaped retinae held together to provide 'X-shaped' combined field of view. Arrows indicate movement of retinae.(A) Spontaneous activity (retinae move more or less unpredictably over scene). (B) Saccades (fixate fields of view on object: black square). (C) Tracking (keeps retinae fixated on moving object: black square). (D) Scanning (newly acquired target (black square) examined by moving the retinal fields of view back and forth over its image while slowly rotating one way then other). Modified after Land (1969b).

with which our own eye move, although we are typically unconscious of the small rotational movements (McIlwain 1996). In salticids, eye tube movements sweep the AM retina in complex patterns over the image coming in through the corneal lens.

Small lateral eye-tube movements allow the salticid to sweep the Layer I staircase over the image to examine an object with a part of the staircase where the object is in-focus. Larger eye movements enable the salticid to sample the larger image projected by the corneal lens, and patterns of movement can be complex. In short, the AM eyes behave, and the behaviour of the eye tubes, like the movements made by our own eyes (Land & Furneaux 1997), may be intimately involved in how salticids process visual information, serving as critical steps in the perception of shape and form (Land 1969b).

Although known for over 70 years (Homann 1928), there has been only one extensive study of how salticids move their eyes. Land (1969b) categorised four types of movement (Fig. 14) from three species of insectivorous salticids (*Phidippus johnsoni, Metaphidippus aeneolus* and *M. harfordi*, each of which appear to have a behavioural repertoire considerably more limited than that of *Portia* spp.). Most eye movement by these species involved the retinae of the two AM eyes moving their fields of view in tandem while held together. The fields of view of the two AM eyes, when held together, forms an 'X' shape with the fields of view of the two foveal regions not quite intersecting (see Fig. 3 & 14). The four movement types are outlined in the following list.

- Wide angle spontaneous scanning movements (Fig. 14a). The centre of the AM retinae wanders at varying speeds over a large horizontal and vertical field. These movements may cover the AM eye's entire visual field, perhaps searching for objects to fix upon.
- Saccades (Fig. 14b). Rapid movements in which the centre of the retinae of both AM eyes move to fixate on some object that has just moved.

- Tracking (Fig. 14c). Movement that keeps the retinae from both AM eyes fixated on a object when it moves.
- Scanning (Fig. 14d). Occurs after the AM retinae fixate on a new target. In this, the most complex of the four movement patterns, the AM retinae move quickly back and forth (0.5-1 Hz) across the image of an object (approximately the width of the Layer I staircase), all the while more slowly rotating through an arc of about 50°.

There have been no comparable studies of how *Portia*'s AM eyes move. However, it is known that the AM eyes of *Portia fimbriata* are more active (i.e., they tend to move almost continuously) than those of any other species that has been examined (Williams & McIntyre 1980). Study of how *Portia*'s eye tubes move might be especially informative about the processes that underlie visual perception.

Conclusion

Salticids have unique, complex eyes (Fig. 14) that support spatial acuities exceeding that known for any other animal of comparable size (Land 1985a; Land & Fernald 1992). The maximum resolving power (visual angle) of *Portia fimbriata*'s eyes (2.4 min arc; Williams & McIntyre 1980) is tenfold better than that of the most visually-acute insect known (the dragonfly *Sympetrum striolatum*, 0.4°; Labhart & Nilsson 1995) and only four times worse that of humans (0.01°; Miller 1979).

Perhaps excellent eyesight is critical in allowing these spiders to behave in a manner that defies their stature. If this is the case, understanding how eyes function is a vital step on the road to understanding how *Portia* and other salticids achieve such surprising feats of problem solving despite having such a small brain (Dukas & Real 1992).

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Chapter 3. The virtual lure presentation system

Introduction

Before we can understand the mechanisms that underlie cognition in salticids we need to understand of the sensory mechanisms by which these salticids acquire the information used when making decisions. This can be envisaged as the external inputs. As vision is well established as the primary sensory modality in salticids, clarifying the nature, potentials and limitations of the mechanisms that underlie visual perception is especially important. Here I explain new tools I have developed for investigating questions about visual perception in salticids, and especially in *Portia*.

My initial goal has been to identify optical cues that trigger and modify the behaviour of *Portia* in encounters with other animals. Particular attention has been given to cues by which *Portia* discriminates between different types o f animals. Typical experimental designs have been based on presenting *Portia* with models of the animals (often called lures). By modifying the appearance of the lure, and recording the way in which the salticid reacts, or fails to react, we can potentially find what features define the cues.

Types of lures

In previous studies, the kinds of lures used for testing salticid visual perception have varied widely. For example, live animals (Edwards 1980, Chapters 4 & 5), dead animals (Drees 1952; Jackson & Tarsitano 1993; Chapters 6 & 9), two-dimensional drawing (Heil 1936; Crane 1949; Drees 1952; Forster 1985), and three-dimensional lures constructed from modelling clay and wire (Drees 1952), have all been used. Each of these types of lures has its own specific advantages and disadvantages. Perhaps taking a lead from studies on bees highly abstract lures have been used in some investigations, usually two-dimensional drawings that typically had no more than a passing resemblance to real animals (Heil 1936; Crane

1949; Drees 1952; Forster 1985). However, more recent studies on *Portia* spp. (Jackson & Tarsitano 1993; Li & Jackson 1996) have favoured lures that are either living animals (live lures) or dead animals that have been mounted in lifelike posture (dead lures). Dead lures are more or less realistic in form, but only live lures are realistic in both form and movement. Each individual body part and the body as a whole move naturally. However, there are disadvantages in using live lures, the most obvious being difficulty in gaining any reasonable measure of control over the movement patterns of live animals. Standardizing movement cues being virtually impossible, working with dead lures may seem to be a better option. With dead lures, highly standardized movement is possible, but the movement achieved tends to be highly non-realistic. Two-dimensional drawings can also be moved but here the problems are even more severe. For two-dimensional lures, only movement in two dimensions tends to be practicable. Three-dimensional lures made from dead animals can , at least, be rotated.

The modifications that can be made to live lures are usually highly limited (e.g., adding tufts of hair or clipping wings). The scope for modifying dead lures is more extensive, but not as extensive as with abstract lures. Some individual body parts (e.g., legs, carapaces, abdomens, etc.) of dead lures can be displaced from their normal position, removed entirely, and even replaced with parts from other animals. However, more fine-grained changes in body parts can be technically challenging and some modifications, for example changing the shape of a salticid lure's principal eyes, would be close to impossible.

Methods used for making dead lures from arthropods

Dead lures used in the experiments in this thesis (Chapters 6 & 9) were constructed by first killing a spider or an insect (subject) by asphyxiation with carbon dioxide gas, then placing it in 80% ethanol for 1 h. The subject was then mounted (using non-shrinking contact cement)

in the centre of one side of a disc-shaped piece of cork (diameter, c. 12.5 mm) and its legs and body manipulated with fine forceps until the subject was in a life-like posture. Any necessary modifications (depending on the experiment) were then made to the subject (e.g., removing legs, painting over features, or adding features). Finally the subject plus the cork was sprayed with a transparent plastic lacquer from an aerosol can for preservation and for elimination of any residual olfactory cues that might still be present on the dead subject.

The end product of this process is a lure that is both odourless and realistic in appearance. Lures contacted by *Portia* can be washed in ethanol without causing damage. However, because these lures are brittle, they are easily damaged by humans and by *Portia*, and they eventually decompose, losing their shape and realistic appearance.

Virtual lure presentation system

The need for a new way of presenting lures to *Portia* arose when by goal became to ask questions about cues provided by features that were difficult or near impossible to alter on a dead lure. For example, I wanted to change the position, size or shape of the principal eyes on salticid lures. Although such changes could potentially be made using two-dimensional drawing-type lures, it was realized that these were unlikely to be suitable because of lack of realism (e.g., they could not be rotated). The development of a virtuallure presentation system became a major part of my thesis research. The aim was to produce a system that combine the advantages of the dead lures, live lures and abstract lures, while avoiding many of the disadvantages of each.

The virtual-lure presentation system (VLPS) displays a computer-designed lure on a two-dimensional screen using a specialized projector. These lures are designed as virtual

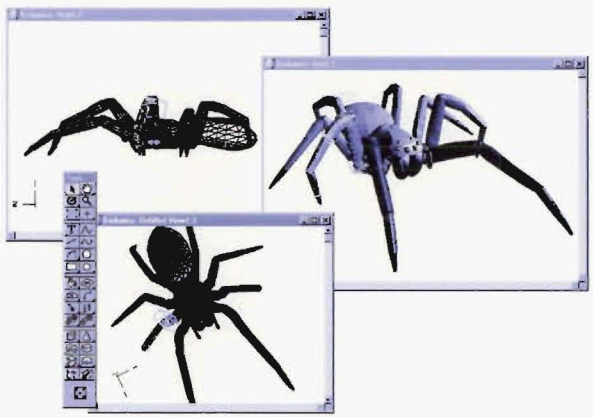
three-dimensional objects within a computer. Almost every important aspect of the virtual lures's appearance and behaviour is under the researcher's control.

Three parts make up the VLPS, a 3D modelling package, an experimental test harness that provides interactivity with the lures and a presentation device, in this case a computer projector (Fig. 1). Each of these three components is essentially independent from the others and each could potentially be replaced with a suitable alternative (e.g., different 3D modelling program, or a different output device like a TV) without disturbing the way in which the rest of the system operates. A 450MHz Pentium III PC computer with 128MB RAM and running Microsoft Windows 98 powers the current VLPS. A less powerful computer system would not be practical.

Each of the three components has its basis in products bought "off the shelf" and then further developed and tuned to make the final system. The original products were:

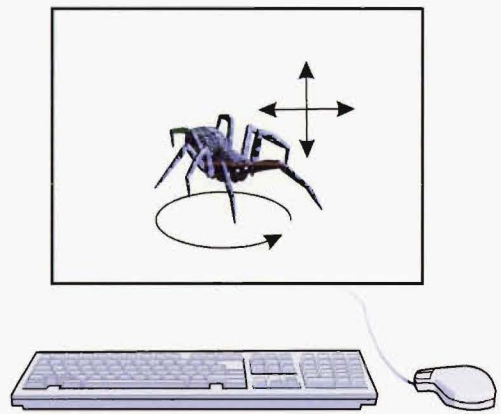
- Macromedia Extreme 3D 2.0 drawing package;
- Macromedia Director 6.5 (a powerful multimedia programming environment used to write the program for presenting virtual lures);
- a Telex P400 LCD projector (output resolution 800x600 in 24 bit colour).

One of these products, Extreme 3D, as of mid-1999 is no longer marketed. However, it is also the easiest of the products to replace. Lures of specific animals were initially designed and 'built' using Extreme 3D. A realistic external appearance can be ensured because the exact shape of each part of the body (leg, wing etc.) can be accurately copied from dead specimens and illustrations from taxonomic references. Surface details (e.g., texture and pattern) can be taken directly from photographs or video of the lures' subject and applied to specific body parts. Posture and body-movement pattern can be copied exactly from real life or video footage of live animals. An unmodified virtual lure can then be converted into an



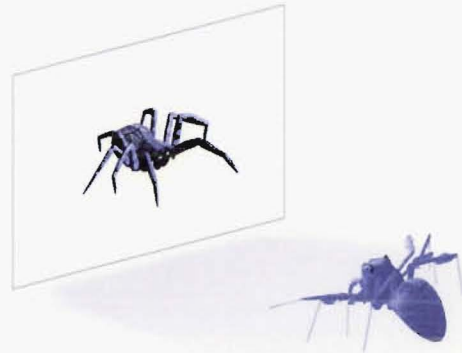
Virtual 3D lure

external appearance
and movement patterns
are under complete
control of the designer
and all properties of
the lure can be changed



User-controlled test-harness program

keyboard and mouse are
used to control the lure's
appearance and behaviour



Presentation system

a modified-computer
projector images the test
harness on a small screen

Portia interacts with a lure
that is under the control
of the researcher

Figure 1. Three components of the Virtual Lure Presentation System. **Left.** Virtual 3D lures are designed in a modelling program from taxonomic drawings, dead and live specimens. **Middle.** During tests, behaviour and appearance of lures are under control of computer or researcher. **Right.** Behaving lures are presented to *Portia* at life size on a small projector screen.

experimentally modified lure. A finished virtual 3D lure is packaged as a series of animated sequences which is then included in a custom built test-harness program that adds interactivity and is used to run specific tests.

The test-harness program developed for testing virtual lures with *Portia* was written in a language called Lingo that makes up part of the Macromedia Director multimedia programming environment. The test harness is designed to be customised for specific experiments and then compiled as a stand-alone program.

Running tests using the VLPS

Running tests requires only the animated lure files, the test-harness program, and the projector. Neither Extreme 3D nor Director are required for any purpose other than for designing lures and writing and initially setting up the test-harness program code. Therefore, once complete, any particular test-harness and its associated animated lure files can be taken to other labs and used on other computers.

The test-harness in Chapter 7 was designed to display a series of lures that can each be moved around the screen and rotated to show their sides and back. While testing a researcher can use the keyboard to switch between different lures (Fig. 2a) and, using the computer mouse alone, move the lure horizontally and vertically on the screen (Fig. 2b) or rotate it in either direction (Fig. 2c). The speed of lure rotation is also under control of the mouse (Fig. 2d). Rotation can be suddenly stopped (Fig. 2e) or the lure can be suddenly turned to face forwards (Fig. 2f). Using the mouse alone to control lure behaviour keeps one hand free for recording *Portia*'s responses.

The third component of the VLPS, the projector, is used only during tests. Commercial projectors are designed to project an image on to a large screen. For the VLPS

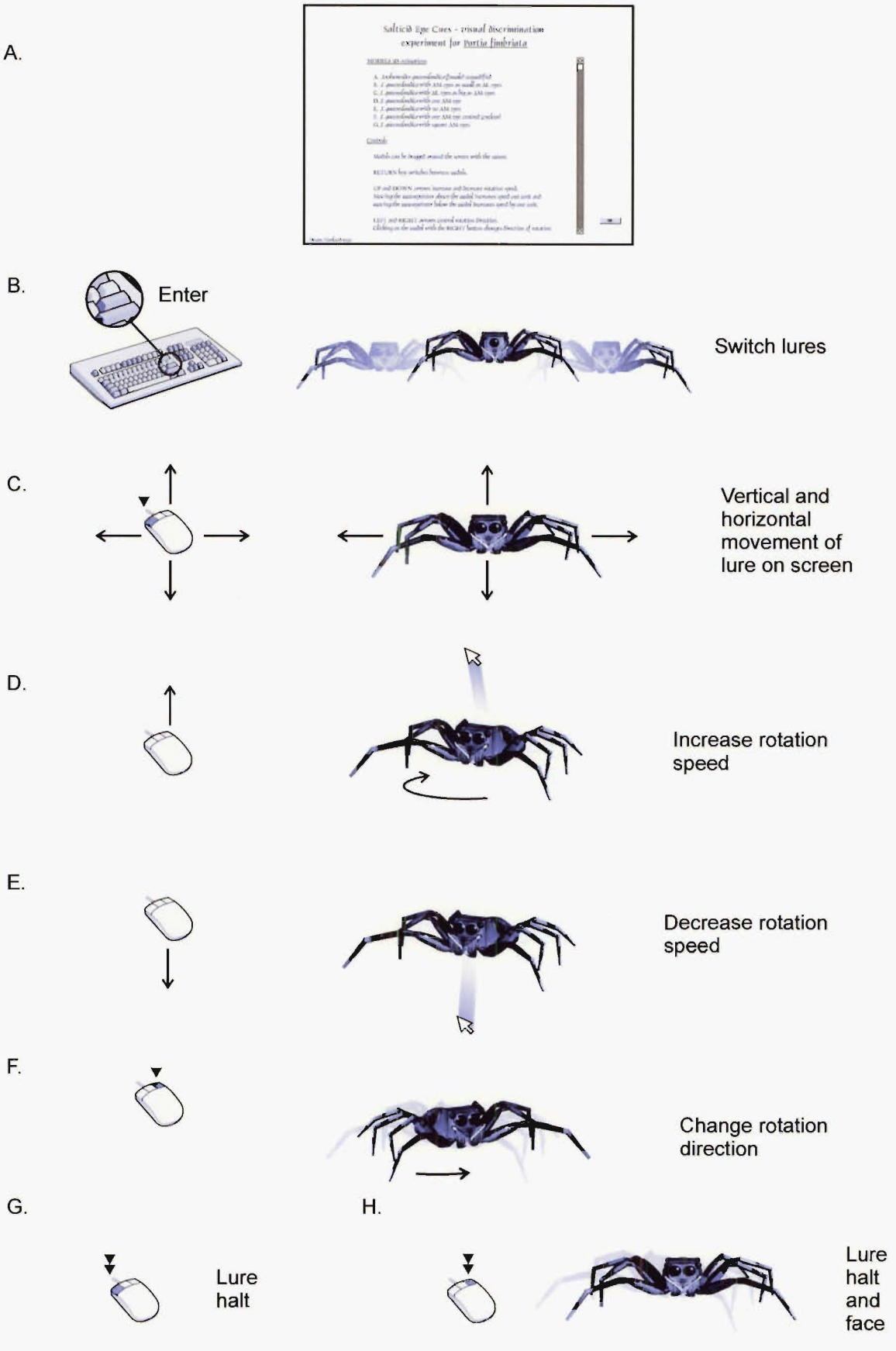


Figure 2. Using the test harness program. **A**. Initial screen displays experimental instructions. Push button to continue. **B**. Enter key switches between lures. **C**. Drag lure around screen using mouse. **D**. Moving mouse pointer above lure (no click) increases lure's rotation speed 10%. **E**. Moving mouse pointer below lure slows rotation 10%. **F**. Single click right mouse button changes rotation direction. **G**. Double clicking left mouse button suddenly halts rotation. **H**. Double clicking right mouse button halts lure rotation and turns lure to face forwards.

the aim was, instead, to project an image onto a small screen. This is because lures must be presented to *Portia* at life size. The image from a commercial projector can be reduced to the desired size by either replacing the lens system or augmenting the existing lens system with an additional array of reducing lenses. Unfortunately, regardless of method, reducing the size of the image introduces, as a side effect, an increase in image brightness. Increased brightness is typically so great that all details of the projected image (lure) are lost in the glare. Reducing the image brightness to a realistic level can be achieved by either the inclusion of light stops (e.g., an adjustable iris) within the lens system or, if this is impossible, neutral-density filters.

The projector in the current VLPS had a lens array that could neither be removed nor modified by adding brightness stops. The problem was solved by a custom lens and filter array designed to fit in front of the projector's existing lens array. This custom array considerably reduced both the size and brightness of the image from the projector. The reduced image comes into focus on a fine screen and its brightness is then reduced further (and contrast increased) by more neutral density filters (see section on technical details and Fig. 29 for details of the design of the custom lens and filter array).

What is seen from the outside is a small screen that is essentially the same as the computer screen. Lures can be presented on this screen in the same way as on the main computer monitor. The only remaining requirement is a suitable viewing platform for *Portia.*

The platform used in Chapter 7 was a wire frame (65 mm wide and 80 mm long) over which multiple layers of spider web (from *Badumna longinquus* (L. Koch)) had been stretched. Washing frames and webs in 80% ethanol before they are used each time removed chemicals left by other spiders that might act as additional confounding cues for *Portia.*

A test begins when *Portia* emerges from a vial (diameter 10 mm) at the far side of the platform(Fig. 3a). Coming out of the vial, *Portia* is facing toward the screen. To approach the

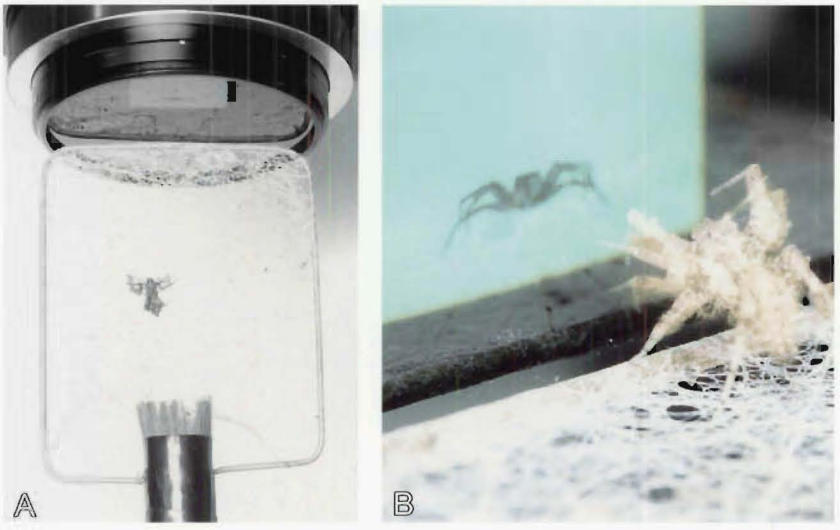


Figure 3. *Portia* stalks a virtual lure. **A**. Top view. *Portia* stalks across platform of webbing from vial (bottom) to projector screen (top). **B**. *Portia* peers through glass barrier at lure (slightly out of focus). *Portia*'s blurred leg movements: frustrated attempts to get closer to lure.

lure, *Portia* must transverse the web. While moving across the web, tests and observations on *Portia*, based on the specific nature of the lure, can be carried out (Fig. 3b).

Effectiveness of the VLPS

Compared with the kinds of lures used previously, the VLPS is designed to allow a higher degree of control over modifications in appearance. The questions investigated are typically the same as in the past, but with fewer of the limitations earlier methods imposed.

A first step was to determine whether *Portia* would react to a virtual lure as it would to an equivalent dead lure. *Portia* was tested with three different virtual lures corresponding to three species of prey spider, *Badumna longinquus* (Desidae), *Pholcus phalangioides* (Pholcidae) and *Jacksonoides queenslandicus* (Salticidae). All three were readily stalked. Being araneophagic, *Portia* an atypical salticid. However, three species of more or less typically insectivorous salticids, *Euophrys parvula*, *Trite planiceps* and *J. queenslandicus*, were also tested. Each readily oriented toward, stalked and repeatedly leapt at house-fly lures from the VLPS. However, these observations are, by themselves, not satisfactory evidence that these salticids actually perceive the lures as a specific type of prey rather than just prey in general (e.g., a simple black dot might potentially also be reacted to as prey).

What needs to be known is if *Portia*, and other salticids, can discriminate between different virtual lures (i.e., can we elicit lure-specific behaviour?). Even more, any lure-specific behaviour should correspond to behaviour normally observed when *Portia*, or another salticid, encounters the animal represented by the virtual lure. For example, if the virtual lure is of an adult *Portia*, we would predict that an adult *Portia* presented with this lure would display as if the lure was a conspecific. This kind of evidence was obtained when *J. queenslandicus* adult males were tested, and seen performing courtship displays in front

of, a virtual lure corresponding to a *J. queenslandicus* adult female. More evidence came from *Portia fimbriata*'s reaction to this same virtual lure.

Details will not be given here, but three stalking styles are discernible for *P. fimbriata* from Queensland, Australia (see Chapters 5 - 7): cryptic, partially cryptic, and ordinary. Cryptic stalking is adopted only when the prey is a salticid. To gauge the effectiveness of the VLPS, we can compare *P. fimbriata*'s reaction to *J. queenslandicus* lures constructed from dead specimens (presented on ramp, see Chapter 6) and those from the VLPS, with adoption of cryptic stalking being evidence that a lure is perceived as being a salticid prey.

Two types of data can be expected for testing *P. fimbriata* with each type of lure. Tendency to stalk the lure can be found by counting the number of *P. fimbriata* that stalk each *J. queenslandicus* lure (Table 1). The style of stalking adopted by those *P. fimbriata* that did begin stalking forms a second data set (Table 2).

We find that there is a significant difference between the number of *P. fimbriata* that reacted to virtual lures compared to dead lures. However, there is no significant difference in stalking styles adopted between those *P. fimbriata* that stalked the virtual lure and those that stalked the dead lure.

One possible conclusion that can be drawn from these comparisons is that *P. fimbriata* perceives virtual *J. queenslandicus* lures in the same way as dead *J. queenslandicus* lures, but the chance of a virtual lure being perceived at all is lower than for dead lures. This conclusion is backed up by observations of the behaviour of many *P. fimbriata* that did not react to lures. Of those that did not react to the virtual lure, 55% did not even orient toward the lure and so probably, at no point, got an opportunity to identify what the lure was. This suggests that the ability of *P. fimbriata*'s secondary eyes to detect motion of virtual lures is reduced compared to their ability to detect the motion of solid objects.

Irrespective of why the tendency to respond to virtual lures was low, that *Portia* and other salticids react to virtual lures in the same way as dead lures means that the VLPS is a potentially useful tool for investigating the processes that underlie visual perception.

Table 1. *P. fimbriata*'s reaction tendency with lures

	N	Stalk	No stalk	test of independence
Virtual *J. queenslandicus* lure	58	64%	36%	P<0.01
Dead *J. queenslandicus* lure	224	83%	17%	
Virtual *B. longinquus* lure	16	75%	25%	P<0.05
Dead *B. longinquus* lure	37	97%	3%	

Table 2. Stalking styles adopted against lures

	N	Cryptic stalk	Partial cryptic stalk	Ordinary stalk
Virtual *J. queenslandicus* lure	39	67%	25%	8%
Dead *J. queenslandicus* lure	186	82%	14%	4%

Development of virtual 3D lures and test-harness program

One aim of this chapter is simply to describe the VLPS, but a second aim is to describe the process by which virtual lures are constructed and the test-harness program adapted to different testing scenarios. This chapter is not only a record of what I have achieved as a major aim of my study but is also a guide for the use and further development of this research tool. The following sections outline how to construct a virtual lure using Extreme 3D 2,

although many of the techniques apply to any 3D modelling software, and how to include a finished lure in the test-harness software.

Constructing a lure using Extreme 3D

Virtual lures are stored in the computer as numbers. These numbers represent points in space that define the vertices of polygons. All virtual 3D lures are constructed of objects made up of polygons. However, objects drawn in Extreme 3D do not appear on screen (or projector) as made up of distinct polygons because a filling formula is applied. Called rendering, this formula fills in the surface between polygon vertices and can fill in a smooth surface between polygons.

For complex objects, the rendering process can be slow. This means there is a trade off between the amount of detail and the time taken to render an object. Extreme 3D provides multiple styles of rendering objects from crude but fast (e.g., drawing the actual polygons) to the extremely slow but highly smoothed. A relatively fast style is typically used for drawing lures and the highly detailed style tends to be used only during exportation of a final result.

Building and editing objects in Extreme 3D is, at its most basic level, always a case of manipulating polygons by adjusting the positions of their vertices and edges. However, in addition to manipulating individual vertices, drawing packages, such as Extreme 3D, include tools for manipulating polygons by editing many vertices and edges at the same time. Making a lure involves a mixture of manipulating individual vertices and using more sophisticated tools to manipulate many vertices at one time.

A lure is typically made up of a number of custom-shaped objects attached together in a defined way. Five distinct steps make up the process of constructing a lure so that it can be

used in the test-harness program. The first step is to form and shape the individual objects that will make up the lure. For example, when making a lure of a house fly, each segment of each leg, the head, compound eyes, thorax, abdomen, and each wing would be separate custom-shaped objects (Fig. 4a). In what might be called the second step, although it is usually done at the same time as the first, individual body parts are connected (i.e., cemented) together in appropriate order (Fig. 4b). The third step is to add the surface details (e.g., colours, patterns and textures) that give the lure a realistic appearance (Fig. 4c). Animating the lure is the fourth step (Fig. 4d). During this step, movement patterns are defined for individual body parts and for the whole lure.

The final step is to render the finished lure into a 'movie file' suitable for inclusion in the test harness (Fig. 4e). This movie file is a different file from that used by the 3D modelling program to store the lure as polygons. Instead the movie file is stored as a series of two-dimensional pictures that approximate individual frames in a roll of actual movie film.

Techniques used in each of the five steps are described in the following sections. These sections will be written more or less as instructions. However, this will not a general introduction to using Extreme 3D. Instead, most of the techniques described apply to any 3D modelling program. Anyone wishing to construct a virtual lure by following the 'instructions' given here should first turn to a basic introduction to Extreme 3D (or available substitute). Extreme 3D includes a tutorial to help get new users started.

Step 1. Making individual body parts

The process begins with choosing a subject for the lure (e.g., a house fly). Arthropods tend to be relatively convenient animals from which to make lures. Because of their exoskeletons, the external appearance of most arthropods is defined by discrete body parts and appendages delimited by joints in the integument (e.g., each segment of a leg, thorax etc.). Drawing these

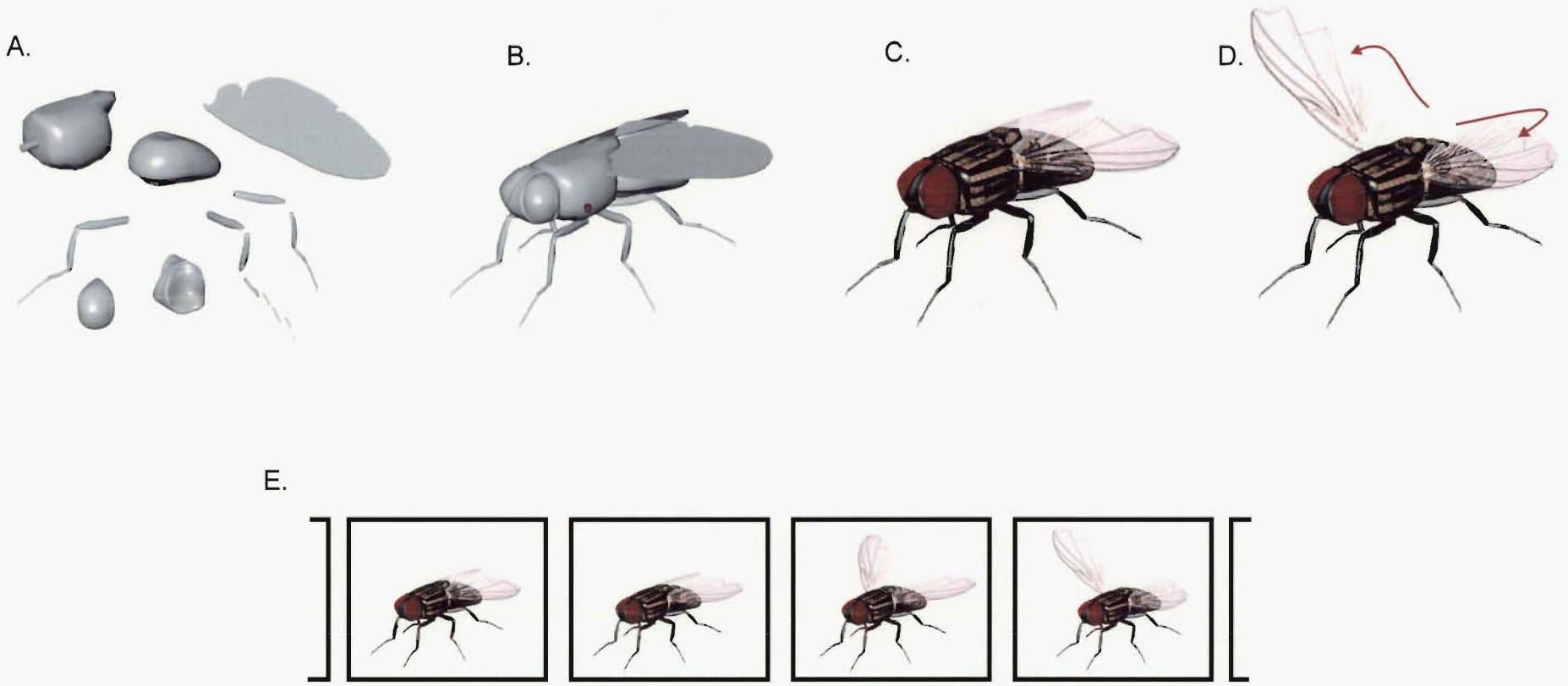


Figure 4. Overview of virtual lure construction process. **A**. Individual body parts copied and scaled from dead and live specimens. **B**. Body parts connected (copied from live specimen) to form lure shape. **C**. External colouring, patterns and surface texture added. Patterns from pictures captured from video of dead specimen and shaped with photo-editing software are wrapped around individual body parts. **D**. Lure animated by moving specific body parts based on frame-by-frame video capture of live behaving specimen. **E**. Final lure rendered into movie for inclusion in test-harness program.

components is the goal of the first step (Fig. 4a), and getting a clear view of each body part and appendage is the first part of this process.

Specimens of the subject are essential if the lure is to be accurate. Having both alive and dead specimens is preferable. Additional material that is useful includes photographs or taxonomic drawings. Individual body parts can be removed from dead specimens, examined, and manipulated under a microscope. These can either be drawn from sight (not recommended) or captured as images and transferred into the computer from where they can be more easily drawn.

Using a video camera or digital still camera to capture images through a microscope or macro lens is a fast one-step method of getting the desired body part into the computer (Fig. 5a). Further modification of captured images using a painting program (e.g., Corel Photopaint or Adobe Photoshop) may then be useful for enhancing critical details (e.g., by making the image sharper; Fig 5b). A captured picture can be displayed in Extreme 3D and used almost like a template for getting the shape of a body part correct along one 2D plane.
In addition to captured images, the remaining dissected parts form an essential part of the drawing process. These are needed to constantly check, by sight, details of the 3D shape and relative scale of each body part.

Extreme 3D has much in common with a 2D drawing program (e.g., Corel Draw). Objects, whether 2D or 3D, are drawn in a window using a set of tools represented by buttons in a tool window. Figure 6 illustrates the basic configuration of the Extreme 3D environment and how a newly drawn object (in this example, a cube) appears. After being drawn, objects can be manipulated with other tools from the tool window, function-specific windows (e.g., object window, surface texture window) and functions available as menu selections. However, Extreme 3D is also different from 2D drawing programs because all objects, and points within objects, are defined on three axes (x, y, z) rather than just

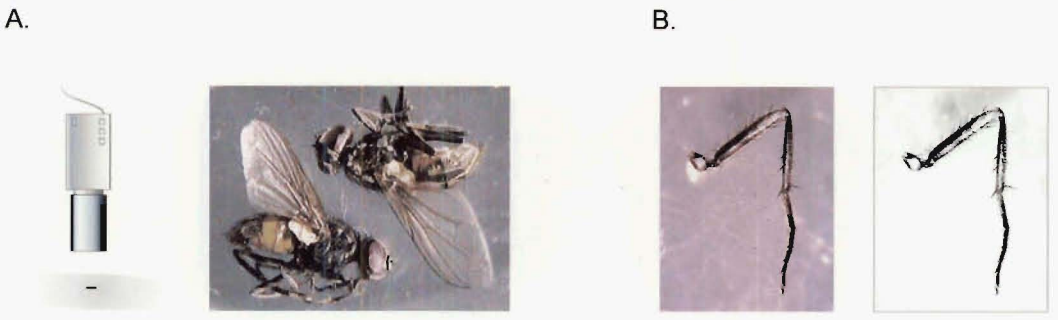


Figure 5. Capturing images of specimens. **A**. Dead specimens (housefly) captured from video. Dissection of specimen provides individual body parts. **B**. Further processing (e.g., adjusting colour depth, contrast, brightness, sharpness etc.) in a photo-editing program can enhance specific features (e.g., hairs).

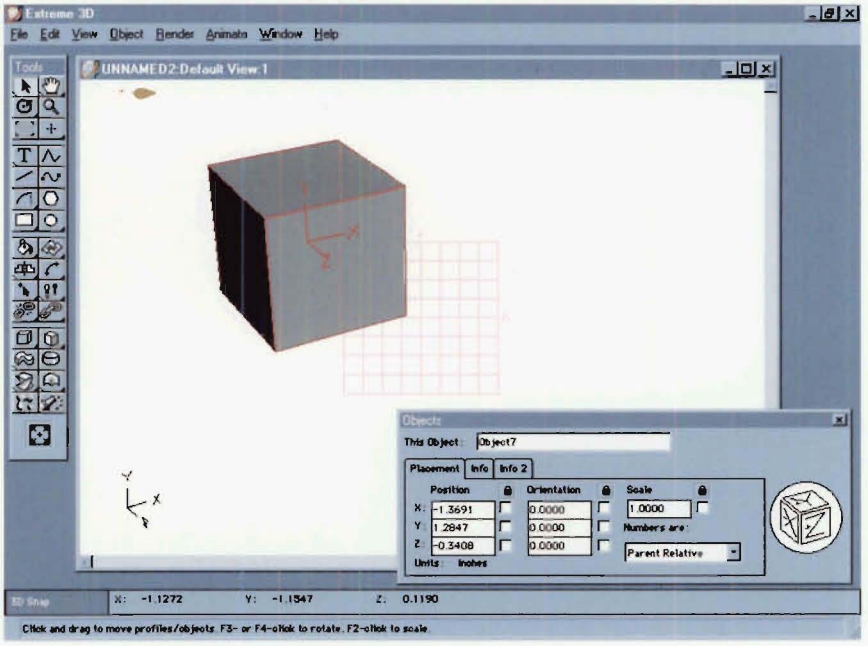


Figure 6. Extreme 3D 2 drawing environment. Objects (e.g., cube) are drawn in a window and manipulated with tools (left side screen) and other windows (e.g., objects, lower right).

two (x, y). Therefore the window in which objects are drawn represents only one 2D view in virtual 3D space. Viewing objects from other angles is easily achieved by either manipulating the object (e.g., rotating) or changing the window's viewpoint in virtual 3D space. Opening multiple windows can allow several concurrent views of an object from different viewpoints (Fig. 7). Ability to visualize objects in virtual 3D space is an essential skill required for building and manipulating virtual 3D lures.

Once specimens have been found and positioned for drawing the next part of the process is to make the basic objects that will become body parts and manipulate them into the desired shape. Extreme 3D provides multiple tools for producing basic 3D objects (Fig. 8), but of these only two, the 'sphere tool' and the 'skin tool', are really useful as starting points for drawing lures. The sphere tool, as its name implies, is used to draw spheres. The skin tool takes a series of 2D objects arranged in 3D space and joins them together by stretching a 3D skin between them. Methods used to construct body parts will be described first for the sphere tool and then for the skin tool.

After drawing a sphere, the aim is to deform and remould it manually into the shape of one specific part of the lure (e.g., cephalothorax). Remoulding a sphere (or any object) involves first opening its defining geometry. Although all objects might be envisaged as being defined by polygons, this level of geometry is not available when a newly created object's geometry is first opened for editing. Instead Extreme 3D has, in addition to polygon level, two higher levels of defining an object's geometry (Fig. 9a). The top level of a sphere's geometry is defined by a semicircular 2D profile lathed around a central axis. This top level geometry can be simplified to a lower level geometry based on individual control points connected by flexible lines. Each control point forms a vertice which can be repositioned relative to other control points. The lines that connect the points define the shape of the sphere. The angle and shape of the curves that connect control points can be adjusted in the

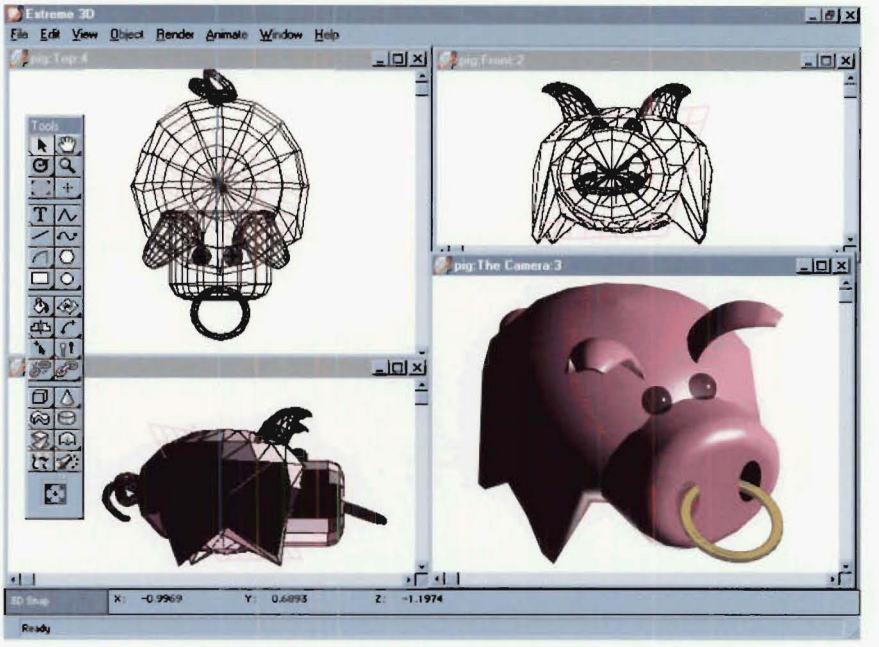


Figure 7. Multiple views and render styles in Extreme 3D. Four windows show the top, right side, front and three quarters profile view of simple 3D drawing in, respectively, wire-frame, faceted wire frame, hidden wire frame and final rendering styles.

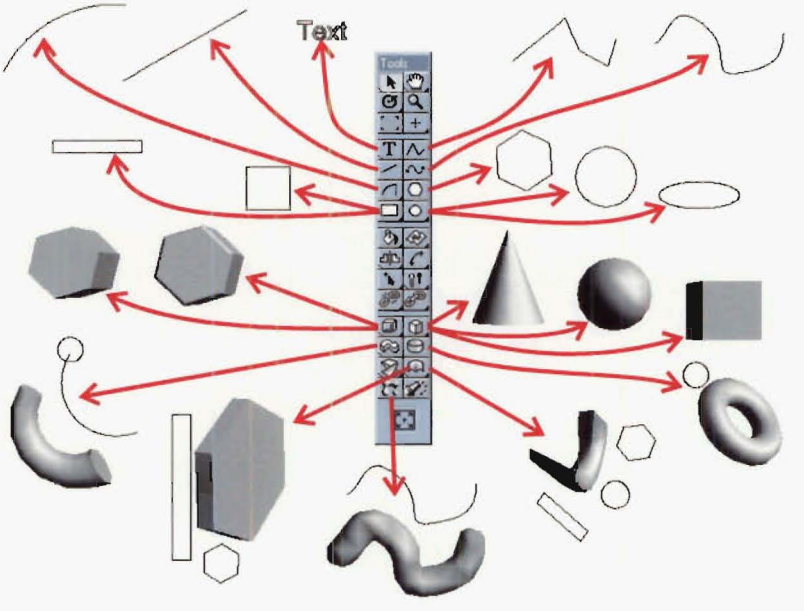


Figure 8. Tools (centre) for creating basic 2D and 3D shapes in Extreme 3D 2. Red arrows connect each tool button with type of created object. Some tools, most of which are in the bottom group of buttons, create 3D objects from manipulating 2D objects.

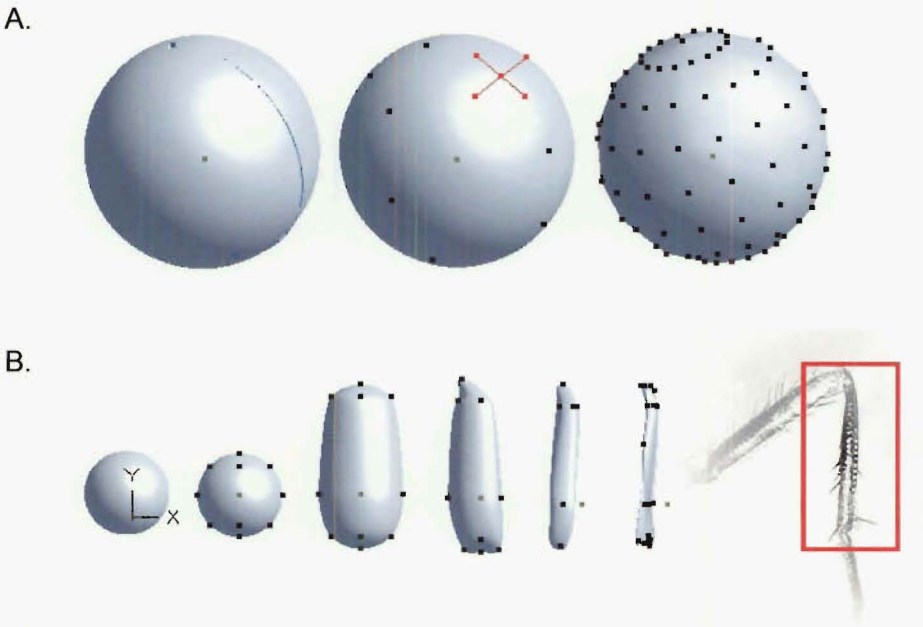


Figure 9. Transformation of basic 3D objects. **A**. Three levels of simplification applied to a basic sphere (drawn with sphere tool). **Left**: before simplification, sphere defined by an arc (blue). **Middle**: after simplifying once, sphere defined by series of Bezier control points (black dots) each defining its relationship with others by relative position and angle (red lines from selected control point). **Right**: after simplifying twice, sphere defined by control points (black dots) defined by position alone. **B**. Transformation of basic sphere into fly's leg segment by manipulation of control points. Left to right: basic sphere; simplified sphere; groups of points pulled vertically; points pushed about to form shape; shape narrowed; close to final shape; goal from video capture.

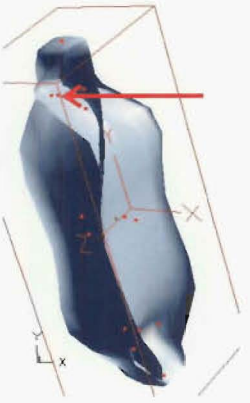


Figure 10. A mess. Object deformed from sphere to resemble elongate body part. Several control points (indicated by arrow) have been accidentally misplaced, rendering object almost beyond repair.

style of a Bezier curve. Simplifying the sphere a second time reveals the lowest level geometry where the control points that define the vertice of each basic polygon is visible. These control points have no associated Bezier-style curves; each is defined only by a position in 3D space. The shape of objects is formed by editing the control points of one of these two lower levels of geometry. However, once an object has been simplified, editing it using any higher level of geometry is no longer possible.

By moving individual control points, and groups of control points selected together, radically reshaping the sphere is possible (Fig. 9b). Besides manipulating existing control points, it maybe necessary to remove control points or even add extra ones. Adding and removing control points works best when done early on.

Making body parts from spheres works best when those body parts are more-or-less spherical to start with. Abdomens, cephalothraxes, heads, and eyes are good examples, but long and thin body parts (e.g., segments of legs) tend to be difficult to draw from a sphere. Drawing objects from a sphere on which the control points will end up very close together increases the risk of mis-aligning adjacent control points and leading to folds and misshapen areas on the object that are difficult to straighten out (Fig. 10). Using the skin tool to draw long thin objects minimises this risk.

Using the skin tool, close matches to the final desired shape can be made. Therefore, fewer modifications at the level of the control points are required. However, there is a minor drawback. Using the skin tool involves investing much more time in the initial set up of the object than is required with the sphere tool.

The skin tool is used to stretch a surface over a series of 2D ribs. Drawing the ribs is the first step in using the skin tool (Fig. 11). Two or more ribs need to be drawn, oriented and aligned before the skin tool is applied. This is not difficult if a picture of the subject body part is loaded into the back of the drawing window, because it can act as a guide for position

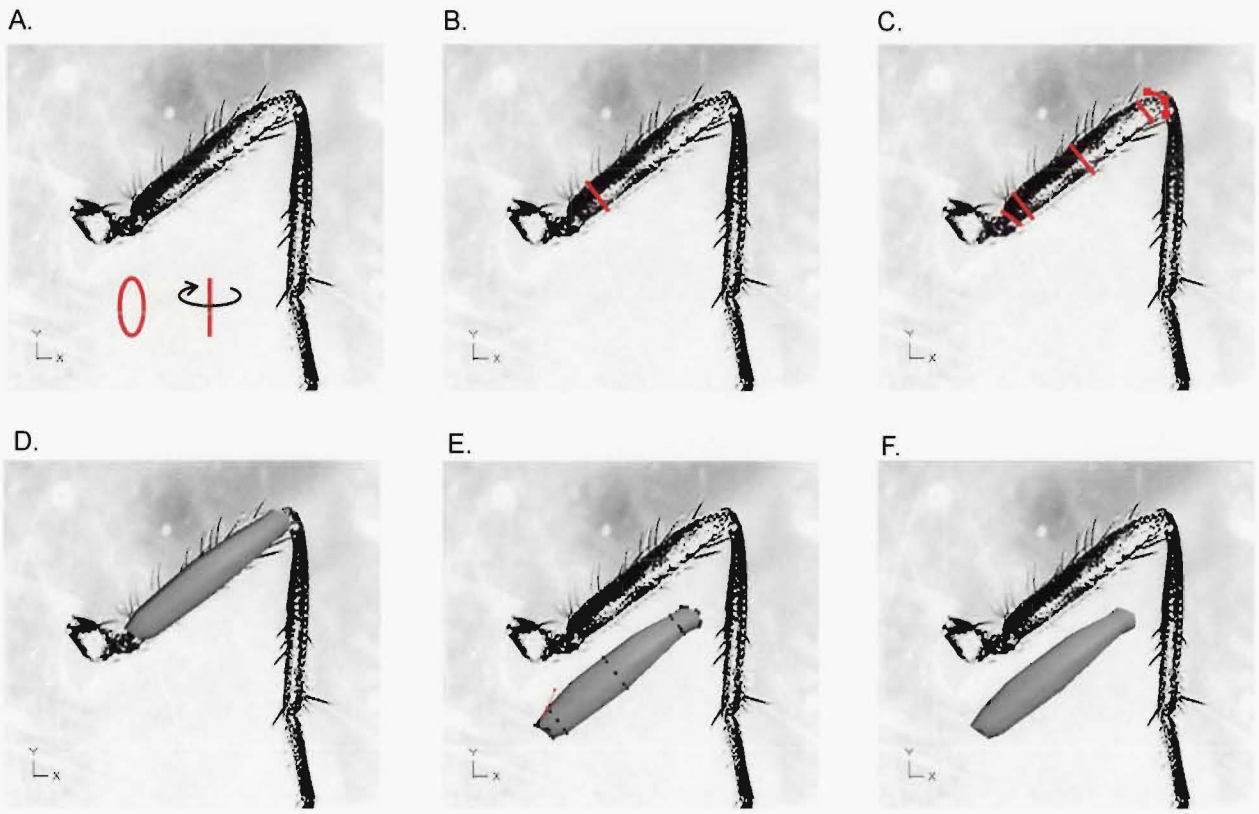


Figure 11. Use of skin tool to make segment of fly leg from video-captured background image. **A**. Oval rib drawn and rotated 90° around Y axis to leg segment's transverse plane (Y-Z plane). **B**. Rib sized and superimposed on picture. **C**. Rib duplicated and duplicates sized, oriented and arranged along leg segment. Top-most rib simplified and deformed to fit end of segment. **D**. skin tool applied to selected ribs. **E**. Skin object's geometry simplified and control points edited to finely mould object to final shape. **F**. final shape.

ing the ribs. Drawing each rib separately is not necessary. One rib, once aligned correctly, can be duplicated and the duplicate positioned independently. Once the skin tool has been applied, the object can be simplified and its geometry modified using the same methods applied when modifying a sphere.

Duplication of objects is not limited to the 2D profiles that make ribs of a skin-tool object. 3D objects can also be duplicated. Duplicating a finished 3D body part can quickly provide a good starting point for the next body part when the second is similar to the first (e.g., leg segments). Mirroring is another form of duplication that is useful for instantly constructing body parts on one side of the lure to match those on the other (e.g., left and right wings or legs).

Tools other than the sphere and skin tools are helpful when constructing certain body parts for lures. For example, wings for insects can be made by extruding a 2D profile (traced wing shape) a very short distance. Hairs and fangs can be made easily by using the sweep tool (Fig. 12). For an example, Fig. 13 depicts many of the finished body parts and indicates the tools used for the construction of each on a house fly lure.

Step 2. Connecting body parts

Connecting a newly built body part involves carefully aligning it next to another existing part and then sticking it on. Aligning a body part with another involves manipulating not just its position, but also its rotation in virtual 3D space. Multiple view windows are often helpful for achieving exact alignment. After alignment, small gaps between body parts can be eliminated by having the objects very slightly overlap. Having two 3D objects that intersect is not a problem because although the 3D objects look solid, they are virtual and can, in part or in whole, share the same virtual space.

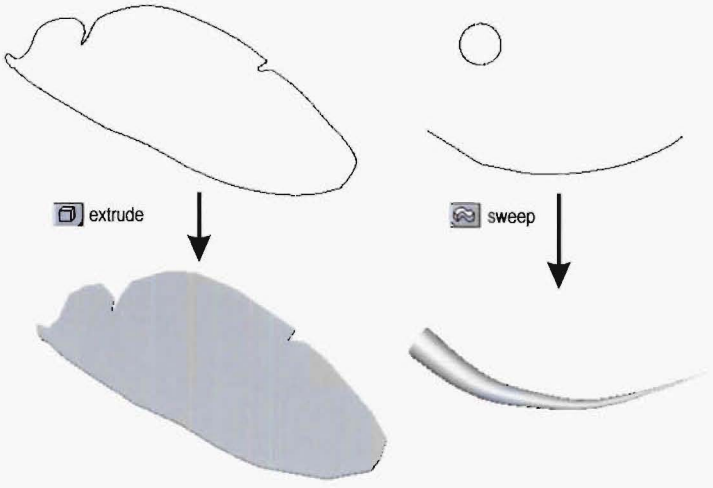


Figure 12. Example of extrude and sweep tools being used. **Left**: fly wing extruded from 2D profile. **Right**: hair made by sweeping circle along curve and narrowing diameter to 0.

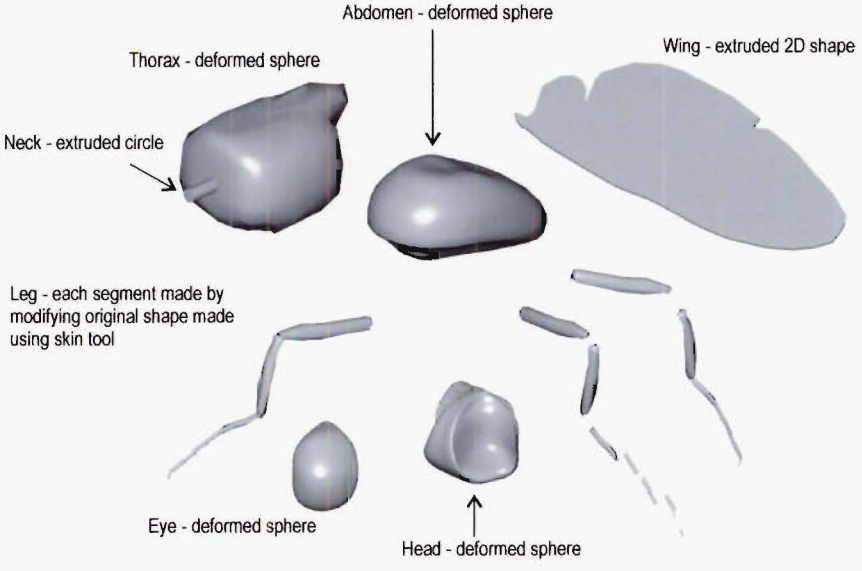


Figure 13. Summary of parts of example lure (house fly) indicating how each part was made.

Extreme 3D provides several different tools, called links, for sticking objects together. A basic link between one object (child object) and another (parent object) ensures that the locked child object will retain its relative spatial position and orientation with the parent object when the parent object is moved or rotated. For example, an abdomen that is linked to a cephalothorax will retain its relative position when the cephalothorax is moved or rotated. Careful linking of body parts is vital if the later step of animating the lure is to be successful.

Basic links are uni-directional; a child object will move with its parent object, but moving a child object does not cause its parent to move. In Extreme 3D a basic link is only one of three types of links that are useful when making lures.

Lock links are bi-directional. Not only is the child object's position and rotation locked relative to the parent, but vice versa also applies. Lock links are useful for those parts of a lure for which posing is not required (e.g., eyes and carapace).

A child object linked to its parent by a ball-joint link cannot be dragged around except by dragging its parent. However, the child object can be rotated about its centre of rotation. Ball-joint links are useful for those parts of a lure that are made to be posed (e.g., on a house-fly lure, segments of the legs, head, and wings). To make a joint it is necessary to move the object's centre of rotation (Fig. 14) to the position around which the joint will move. The effect provides something like the ball and socket joint that connects a human femur to the hip. However, it is not always desirable for joints to move so freely. Typically the joints in the legs of insects and spiders can rotate in only one direction. This can also be replicated for our virtual lure, making the later job of animating the lure easier.

A ball-joint link is the same as a basic link except that the ability to translate the object has been locked in the first three dimensions (x, y and z). Such locking can be controlled directly from the 'object window' (see Fig. 6). The object window also gives access to controls that lock an object's freedom to rotate in the three different planes. By locking the

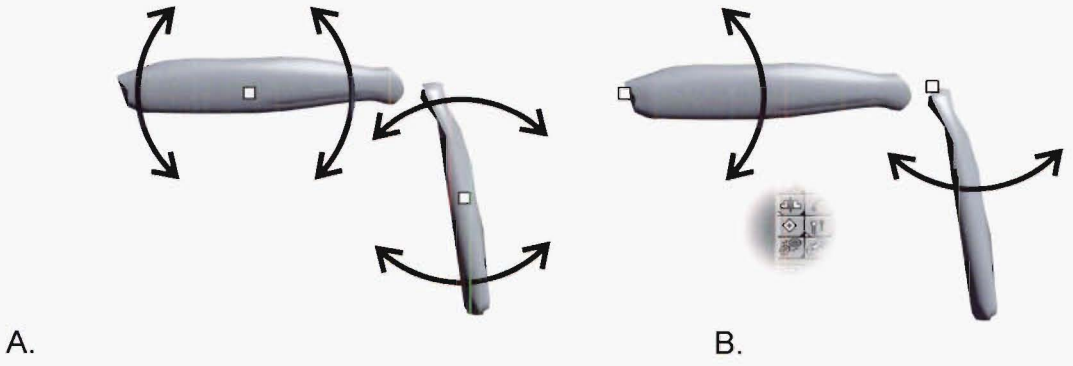


Figure 14. Moving an object's centre of rotation. **A.** Default centre of rotation for two house fly leg segments. **B.** After application of centre of rotation tool (inset).

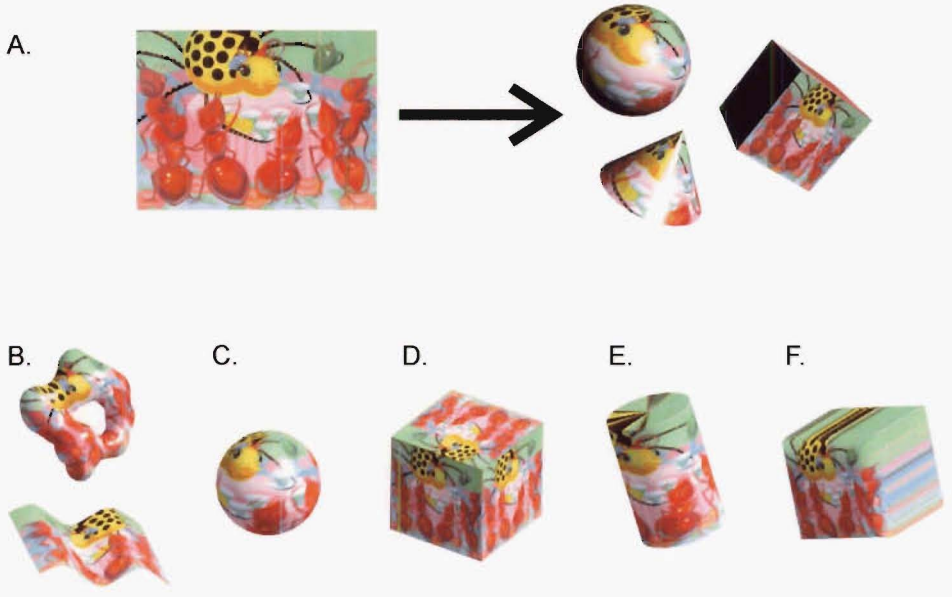


Figure 15. Texture maps. **A. Left**: bitmap illustration from 'Miss Spider's tea party' (David Kirk 1994). **Right**: same bitmap used as texture map, wrapped around sphere, cone and cube. **B.** Intrinsic projection wraps texture map point by point around shape. **C.** Spherical (Mercator) projection wraps texture cylindrically, then pinches ends. **D.** Cubic projection replicates texture map six times, once for each side of cube. **E.** Cylindrical projection. **F.** Linear projection, places texture map along one linear axis.

ability of an object to rotate in two of the dimensions, a simple arthropod-type leg joint can be simulated in a lure.

Step 3. Adding surface detail

The external appearance of the surface of each object in Extreme 3D (e.g., colour, shade, glossiness etc.) is defined by a 'material'. To start with, there is only one material available, 'Gray Plastic', which is applied, by default, to all new objects. Additional materials can be made by either copying the default material or by importing a copy of a basic material into the drawing. Materials are made and edited from the 'materials tool window'. Each material has a group of properties defining its appearance. There are different types of material, each having its own set of properties. After making a new material and giving that material a name (e.g., thorax material), the next step is to modify the properties that define the material. Once made, a new material can be applied to any number of objects (e.g., all leg body parts).

Only two types of material are really useful for making lures - 'Generic+Texture' and 'Mondo Map'. The ubiquitous Gray Plastic is a Generic+Texture material. The basic appearance of all Generic+Texture materials are defined by five variables, colour, specular, roughness, transparency and luminosity. Each of these variables is represented by a colour and a luminance. The colour value defines the base colour of the material (e.g., for a salticid eye material this might be black). Specular and roughness define how virtual lighting illuminates the material. A specular is the reflection of a bright light on an object (e.g., a highlight). In Extreme 3D each defined lighting object makes its own specular. Roughness defines the intensity of a material's specular (the rougher the surface the more light will be scattered). Transparency and luminosity both affect the contrast of the material by, respectively, making the object more transparent and increasing the brightness of all parts of the object.

Generic+Texture materials can also include a bitmap picture. Called a 'texture map', this bitmap picture, when applied to an object, will wrap itself around its surface (Fig. 15a). By default, a wrapped texture map follows the exact contours of the object (intrinsic wrapping) (Fig 15b), but other ways of wrapping a texture map are available. Spherical wrapping (Fig. 15c) is a Mercator projection of the texture map onto an object. Other forms of wrapping are cubic projection (Fig. 15d), cylindrical projection (Fig. 15e) and linear projection (Fig. 15f). For each projection, the position of the texture map, its size, orientation and extent of cover can be adjusted for individual objects using specific texture tools and the object window.

Texture maps potentially allow lures to have highly realistic and detailed surfaces. Scanned photographs or captured video footage of specific body parts from live or dead specimens can form the basis of texture maps. Mondo Map materials are designed specifically for using texture maps and provide a greater degree of control over textures than do Generic+Texture materials.

The variables that control the appearance of a Mondo Map material (i.e., colour, specular, roughness, transparency and luminance) can each be defined by either colour and luminance combinations or by individual texture maps. The base picture that is wrapped around the object's surface (i.e., the colour variable) could be defined by one texture map, and the same or another texture map could be used to define the specular pattern, *et cetera*. Mondo Map also provides a new variable, called the bump map. The bump map defines the surface's bumpiness or texture (i.e., 'texture' in the true meaning of the word).

How difficult making a texture map will be depends on the specific body part for which it is intended. For example, the wing of a house fly is a more-or-less two dimensional structure (i.e., it has no visible sides). A texture map of a house fly wing is a bitmap picture from a single frame of video of an isolated wing (Fig. 16). The map is then used in a Mondo

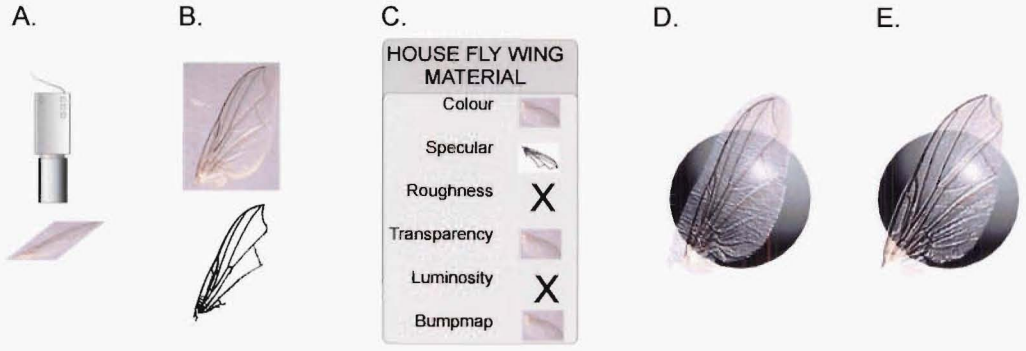
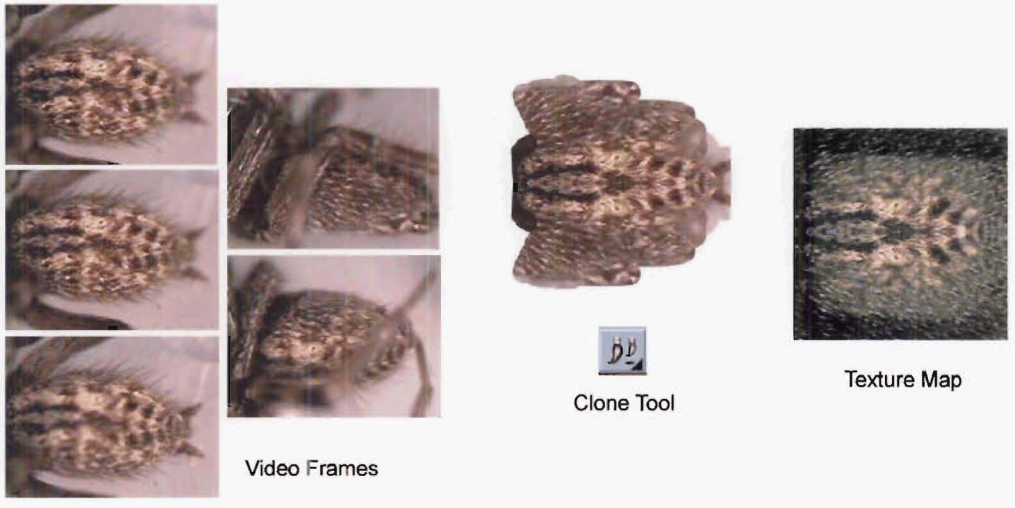


Figure 16. Producing house fly wing texture map. **A**. Captured video frame of wing from dead specimen. **B**. Captured bitmap 'cleaned up' using Photopaint and necessary variations made (black and white skeleton). **C**. Bitmaps define variables in Mondo Map material. **D**. Material applied to house fly wing body part in Extreme 3D. **E**. Texture enlarged slightly and repositioned to fit body part exactly.

A.



B.

Figure 17. Producing 3D texture map of *Badumna longinquus* abdomen. **A. Left**: captured video frames of abdomen of live specimen with different parts in focus. **Middle**: using Photopaint's 'clone tool', in-focus parts are stitched into one image and (**right**) further cloning used to fill gaps with appropriate details. **B**. Finished texture applied using cylindrical projection over top 270° of abdomen body part.

Map material to define pattern, bumpiness, specular, and transparency. This finished material can be applied to the wing body parts using linear projection. Resizing and adjusting the position of the texture map might also be necessary.

Other body parts are more complex because, for some body parts (e.g., a spider's abdomen), viewing the same body part from multiple sides may be required. When this is the case, we need a texture map that will show the sides of the body part that would not be visible at the same time in real life (e.g., top and bottom, front and back, left side and right side). Building a chamber of mirrors that allows a video camera to capture most sides of a body part at one time is one logical solution, but this tends not to be practicable. It is instead easier to stitch together, into one picture, multiple images of one body part using a photo-editing program (e.g., Corel Photopaint, or Adobe Photoshop) (Fig. 17a). Images from different sides of one body part and possibly images focussed on different parts of the same side may be used to make up the texture. When finished, and after any unsightly gaps have been filled, the texture can be used within a material to define colour, bumpiness *et cetera*.

Body parts that have a complex shape require textures to be applied using a carefully chosen projection technique (e.g., cylindrical, spherical, cubic or intrinsic projection). Exactly which projection method is used depends on the shape of the object and the amount of resizing and repositioning needed to make the texture fit (Fig. 17b). Depending on the object's shape, there may be a trade-off between the projection that provides the best fit (e.g., intrinsic projection) and the projection that allows the texture to be most accurately positioned (e.g., cylindrical or linear projections).

The final issue that affects the appearance of materials is lighting. A drawing in Extreme 3D has two default lighting objects (distant light and ambient light) and any number of additional lighting objects can be defined by the user. The properties of each light, for example, its position, brightness and colour, can be defined in the lighting tools window. The

colour, brightness and position of each light affects the final appearance of all objects on which it shines. Adjusting the default ambient and distant lights can give fine control over the overall contrast of a lure, but too little light will not illuminate enough detail on the lure and too much light will reduce the contrast of parts of the lure, also obscuring detail.

Omni lights can be useful for modifying the exact appearance of lures. Unlike distant lights and ambient lights, omni lights can be positioned within the drawing like any other object. Omni lights are useful for highlighting specific regions of the lure and can also be used to darken areas. Setting an omni light to black has the effect of shining 'blackness', thus darkening surrounding surfaces.

Step 4. Adding movement patterns

Animation is the illusion of movement created by rapidly displaying a series of images in which each successive image is slightly different from the last. Each image within an animated sequence is called a frame. Each animated sequence (or movie) has a number of frames which are displayed at a specific frame rate (expressed as frames per second).

Instead of drawing each separate frame in a movie, Extreme 3D allows the user to define specific key frames and then Extreme 3D automatically fills in all movement in between. A simple control panel, similar to that on a VCR, allows the user to play a preview of, and move to different frames within, the movie. Before animation can begin the number of frames in the movie must be defined in the animation control panel.

The number of frames required depends on both the intended length of the animated sequence and the intended frame rate. For example, the virtual-lure based experiments in Chapter 7 were based on animated sequences that were sped up or slowed down during testing. Final movies used showed the lures rotating smoothly around their vertical axes, but the speeds of rotation were changed during tests by either increasing or decreasing a movie's

frame rate within the test harness program. For work of this type, it is important to ensure that, when the lure is made to rotate slowly, each individual frame is not too different from adjacent frames. That is, we do not want the lure to appear to move in small jerks. To avoid this potential problem of jerkiness, the frame rate of the movie produced as an end product from Extreme 3D must be high. The rate used in Chapter 7 was 60 frames per sec. However, in other experiments (e.g., when the objective was that the lure simulated natural movement patterns) frame rates higher than 20-30 frames per second would have been a waste of rendering time and disk storage space.

Animation of lures in Extreme 3D is a matter of changing to a specific frame number and then manipulating the lure (e.g., moving a limb, rotating the lure or changing the shape of a body part). All intervening frames (i.e., between two key frames) are automatically filled with intermediate steps so that, when played, there is a smooth transition from the initial to the manipulated state. Details of this animated sequence can then be further modified using various animation tools (e.g., manipulations can be made in speed variation within the transition and motion path) and also by editing the affected objects within individual transitional frames.

If all the body parts that make up a lure are properly linked, animating movements of any part of the lure is relatively simple (Fig. 18). The same applies to whole lure movements. For example, animating a house-fly lure so that it rotates 360° (Fig. 19a) involves successively, setting the end frame (e.g., 150), selecting the thorax, changing to the end frame, selecting 'autorotate' from the 'animate' menu and setting in the appropriate details. When the resulting sequence is played, the house fly will, in 151 frames, rotate smoothly around its central axis 360°. However, if linking is incomplete, those parts that are not linked, either directly or by descent (e.g., linked to a part that is linked to the thorax etc.), will remain stationary while the remaining linked parts all move with the thorax.

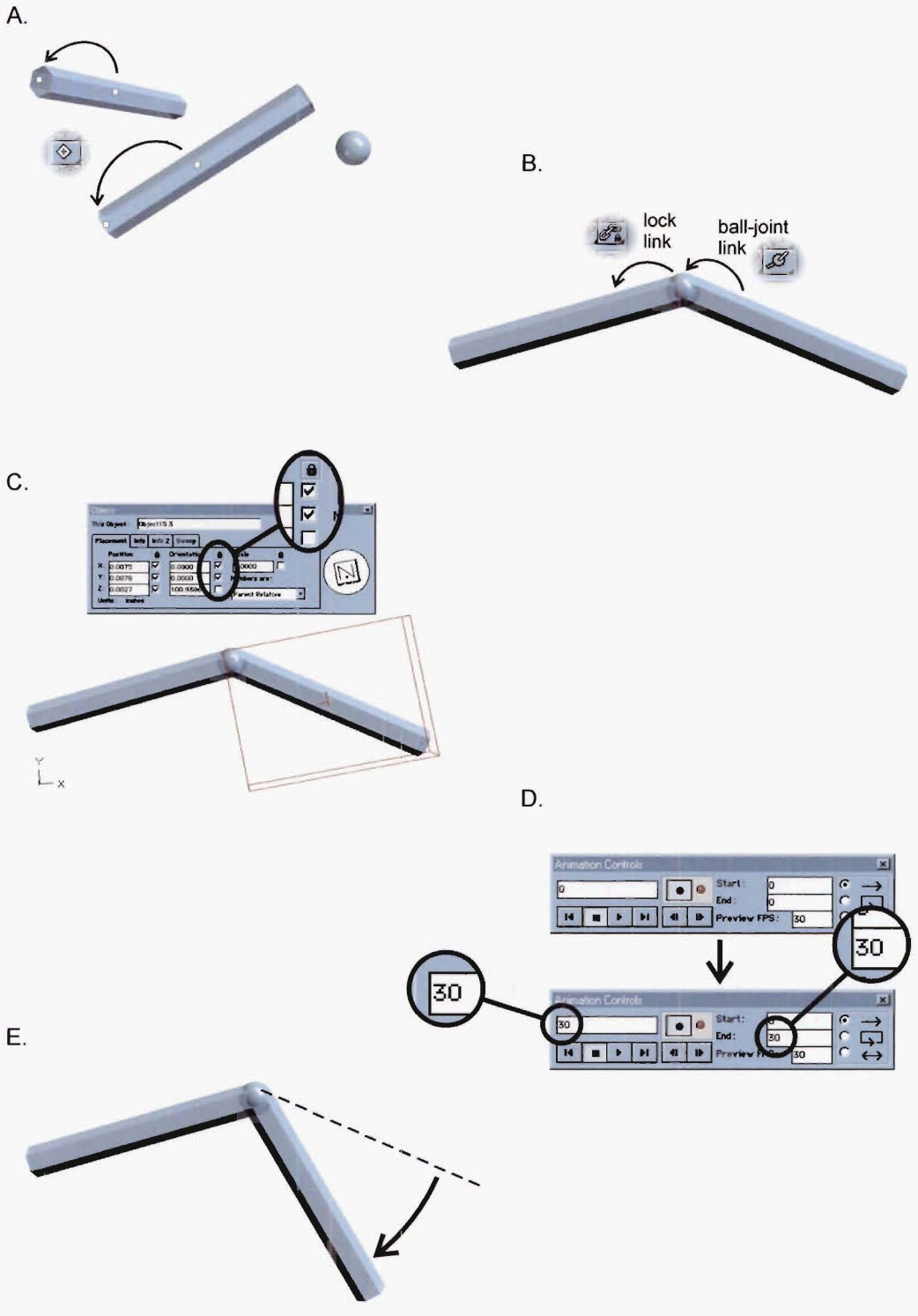
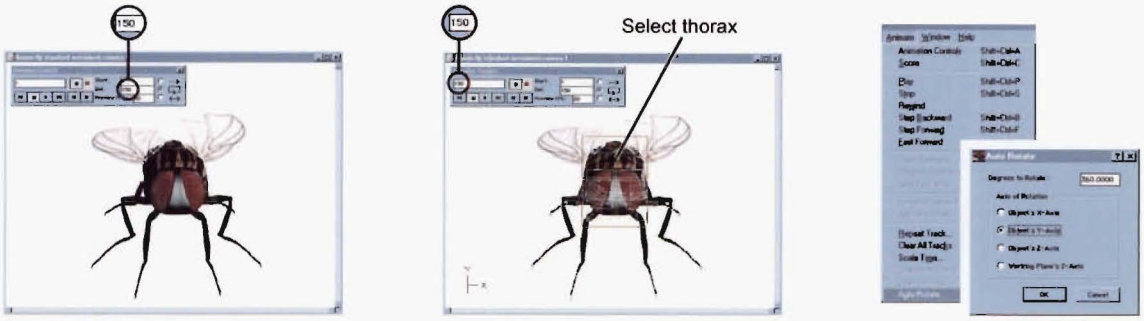


Figure 18. Animating a joint. **A**. Three objects that will form arthropod-style hinge joint. Rotation tool used to move centre of rotations of long sections to ends. **B**. Objects positioned and linked. **C**. Part of limb (right) to be animated is selected. Its rotation constrained from object window. **D**. End frame set on animation controls and current frame set to end frame. **E**. Part of joint to be animated (right) rotated downwards. Joint now animated.

A.



B.

Figure 19. Simple and complex animation of house-fly lure. **A**. Steps towards making a rotating lure. **Left**: set end frame. **Middle**: go to end frame and select thorax (to which all else is linked). **Right**: select auto-rotate and set rotation axis and extent. B. Complex motions of body parts can be copied frame by frame from video footage.

Realistic movements of individual body parts are generated using the same techniques (i.e., changing frames then editing lure), but a large amount of time may be required to replicate exact movement patterns, especially if each frame has to be edited separately. Video footage of live specimens can be used to produce realistic movement patterns by copying the exact position of the specimen's body, frame by frame, from video footage to lure (Fig. 19b)

Step 5. Rendering a movie

Once the lure has been made and animated, it is time to produce the final picture or movie that will be presented through the test harness program to *Portia*. During the previous phases of construction, a relatively fast rendering process was used to convert the polygon vertices that make up the lure's body parts into a picture on the screen. For the final result a much better picture is possible.

In Extreme 3D the final render process can be applied to a single view at any time by selecting 'final render to screen' from the 'render' menu (or by pressing CTRL-R). The command for exporting the lure, including animation, to a bitmap picture or movie file is also found in the render menu. To be compatible with the test harness the exported file must be a movie file (e.g., Microsoft video for windows file or Apple Quicktime file).

Adding a rendered virtual lure to the current test harness program

The current test harness program is designed to allow a researcher to present a movie on the screen, move it about, speed it up, slow it down, suddenly stop it and suddenly stop and rewind it (Fig. 2). The movie will play in an endless loop; that is, the first frame plays directly after the last. Any number of movies can be displayed by the current test harness program, but only one at a time. Director can be used to program in any additional functions,

but in this section the aim is to explain how to add new lures into the existing test harness program.

Within Director the test harness program is made up of two parts (Fig. 20), cast members and sprites. Cast members (Fig. 20a) contain the movies, text and programming code (called lingo). Lingo defines what is possible in the test harness program. Sprites (Fig. 20b) are the expression of those cast members onto part of the screen, called the stage (Fig. 20c). A sprite displays a currently active (or running) cast member. To place a new movie (of a new lure) into the test harness program, we must add a new cast member, edit some parts of the programming code to tell the program that the new cast member exists and, finally, compile the test harness into a stand-alone executable program.

New cast members can be constructed in one of two ways, either by adding information to a blank cast member or by duplicating an existing member and modifying the duplicate. Modifying a duplicated member is the easiest method for adding new lures to the test harness. To duplicate a member, it must be selected in the cast member window and the duplicate command must be chosen from the edit menu (or pressing CTRL-D).

Cast members that contain movies (i.e., lure members) are identified by the small 'movie-camera' icon in the bottom right side of the member's representation (i.e., thumb-nail picture) in the cast member window (Fig. 21a). The icon at the bottom left side of the thumb-nail pictures of lure members indicates associated lingo.

The order in which cast members appear in the cast member window is important. The test harness' programming assumes that the cast members containing the lures always precede, in the cast list, cast members that contain lingo or other details. When a lure member is duplicated, the first modification that is required is to move it (by dragging it with the mouse) until adjacent with one of the existing lure members. The order of the lure members

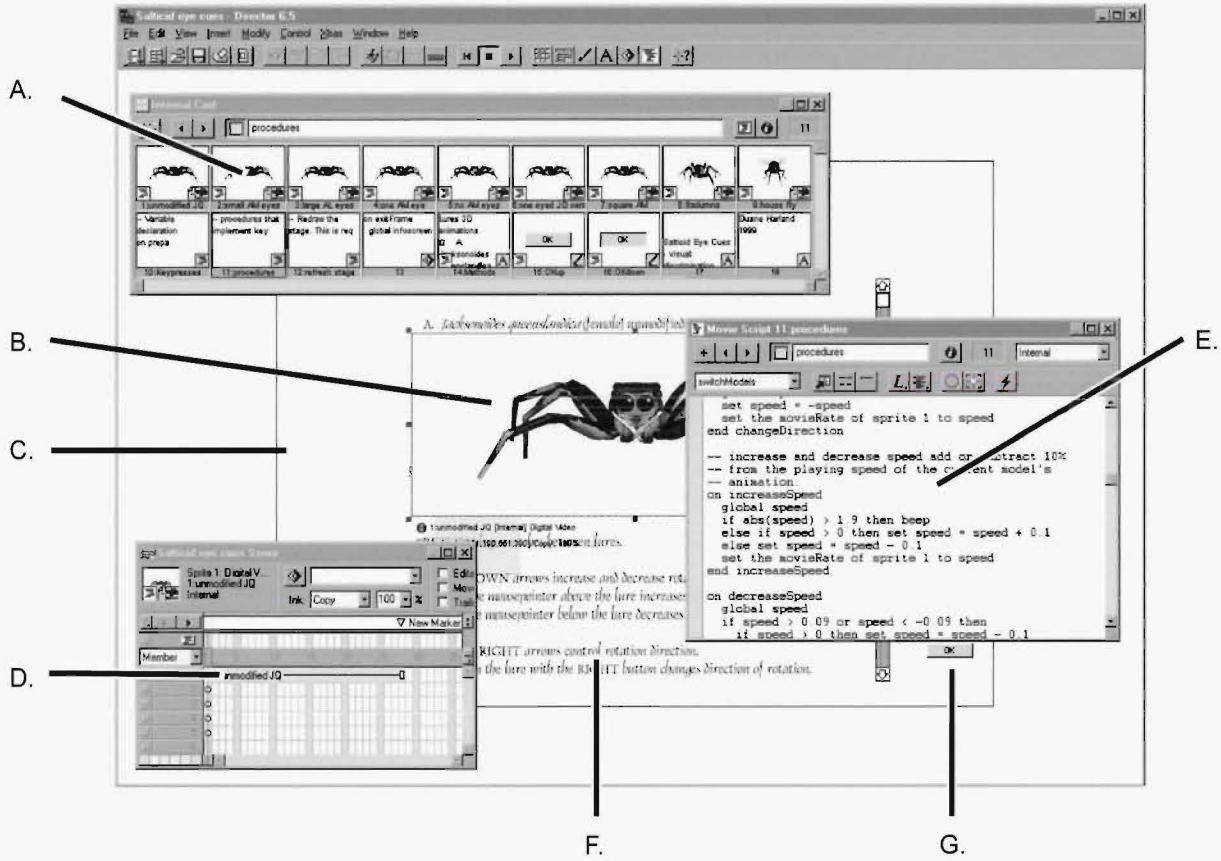


Figure 20. Test harness program in Director. **A**. Cast member (contains one or more of movie, picture, text, sound or code). **B**. Sprite of cast member. **C**. Stage (where sprites are displayed). **D**. Score (sprites over time). **E**. Code from cast member controls sprite behaviour. **F**. Sprite of text cast member. **G**. Sprite of button cast member.

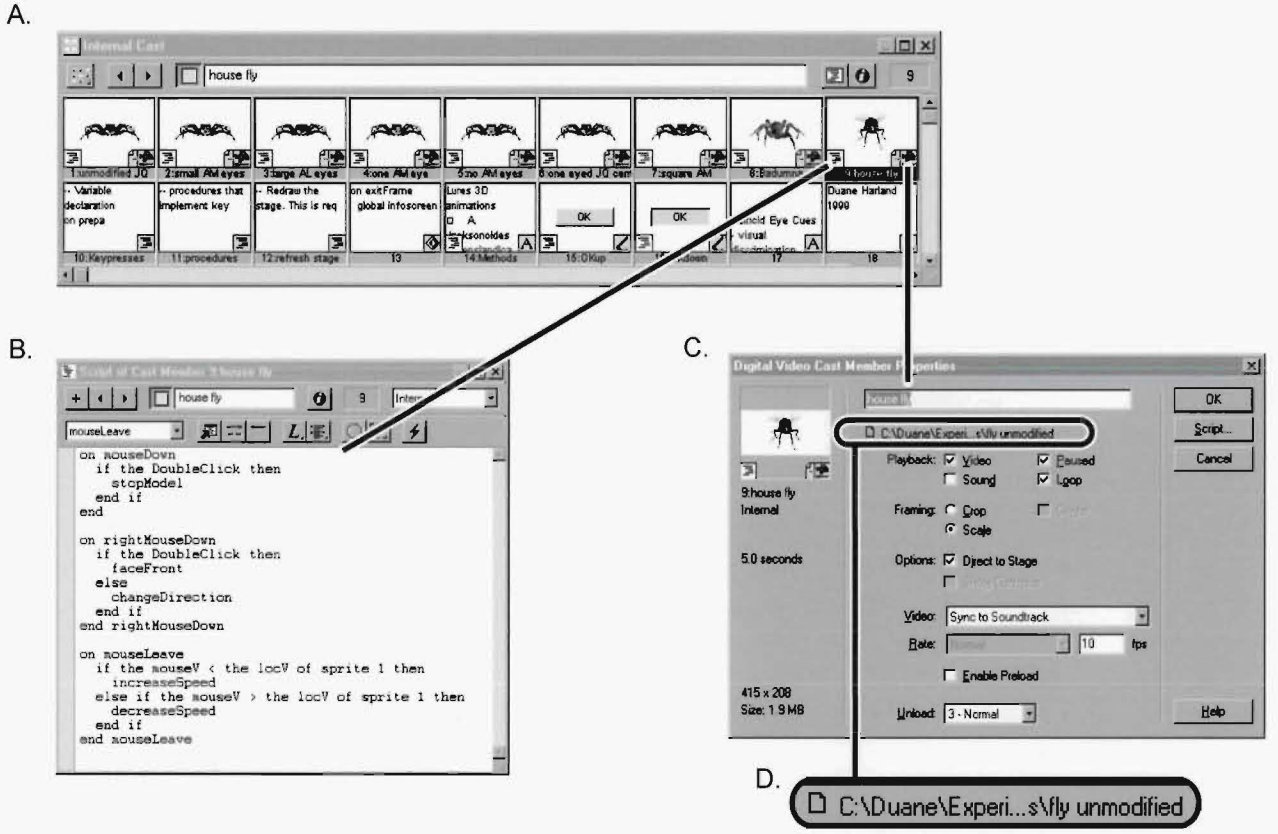


Figure 21. Cast member properties. **A**. Cast member (ordered) list showing thumb-nail pictures. **B**. Programming code for lure cast member. **C**. Settings for lure movie. **D**. File path of movie file contained by cast member.

in the cast member window defines the order in which they will appear when lures are switched between in the finished test harness program (Fig. 2b).

A duplicated lure member has the same movie file, associated lingo (Fig. 21b) and movie settings (Fig. 21c) as the original. Changing the cast member's movie file to the new lure movie should be all that is required. The way to do this is simply to select the file path of the movie in the member's movie settings window and open the movie file of the new lure (Fig. 21c).

Correct running of the test harness program requires information about the number of lure members. The number of lure cast members is held in a variable within a cast member, called 'keypresses', that contains only lingo (Fig. 22). Opening a lingo cast member is achieved by double-clicking on it with the mouse. The variable 'numModels' can then be set to the number of lure members.

There are, in addition to cast members containing movies and just lingo, cast members that contain text. Three such members are found in the test harness and, during program execution, the sprites displaying these members make up the information screen. Adding new lures (or replacing existing lures) may require changing the experimental instructions, experiment title and credits. Changing the contents of a text cast member is achieved by double clicking on its thumb-nail picture and using the text editor.

The final step in the process of adding a new lure to the test harness is to compile a new stand-alone executable file. However, before taking this step, it is wise to run the test harness at least once within Director to check for bugs. Producing an executable is simply a matter of selecting 'make projector' from the file menu, setting the appropriate details (e.g., run full screen) and giving the projector a name.

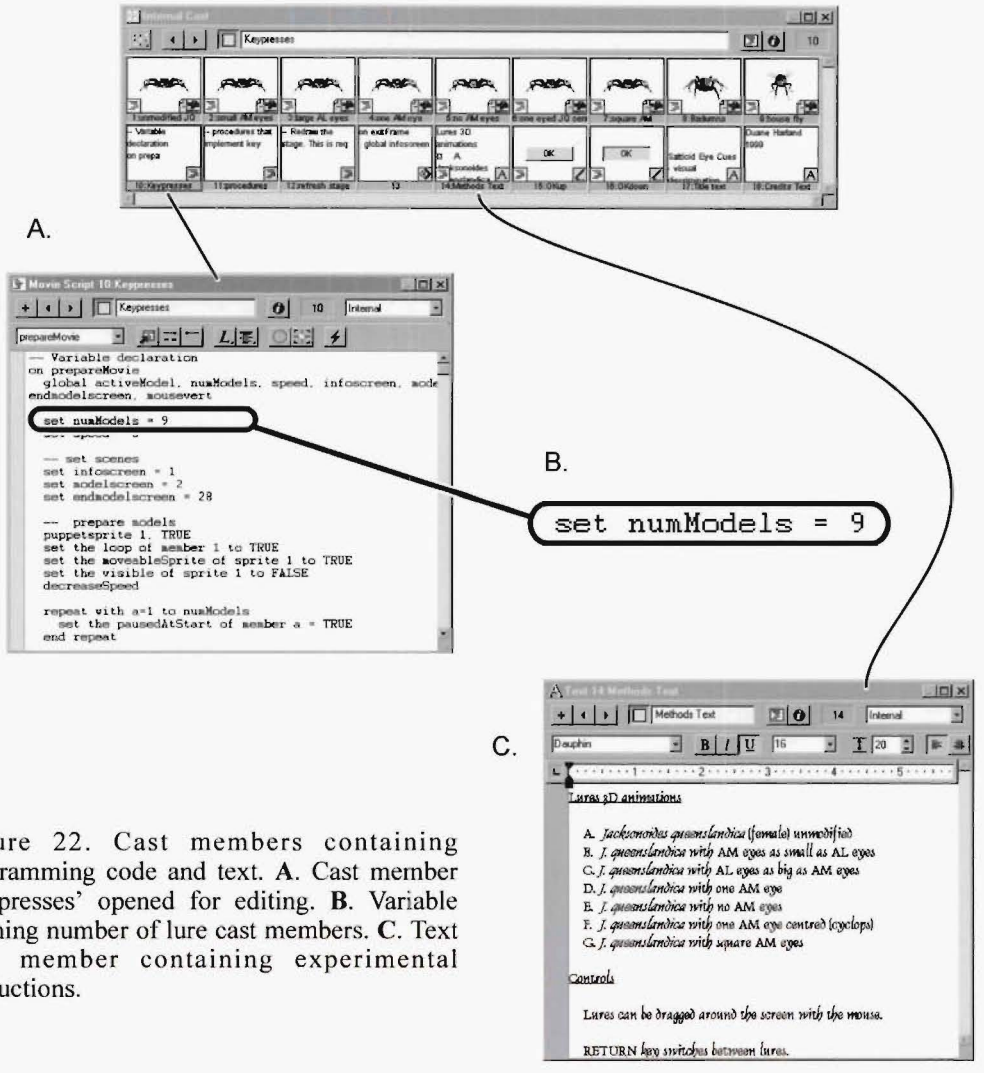


Figure 22. Cast members containing programming code and text. **A.** Cast member 'keypresses' opened for editing. **B.** Variable defining number of lure cast members. **C.** Text cast member containing experimental instructions.

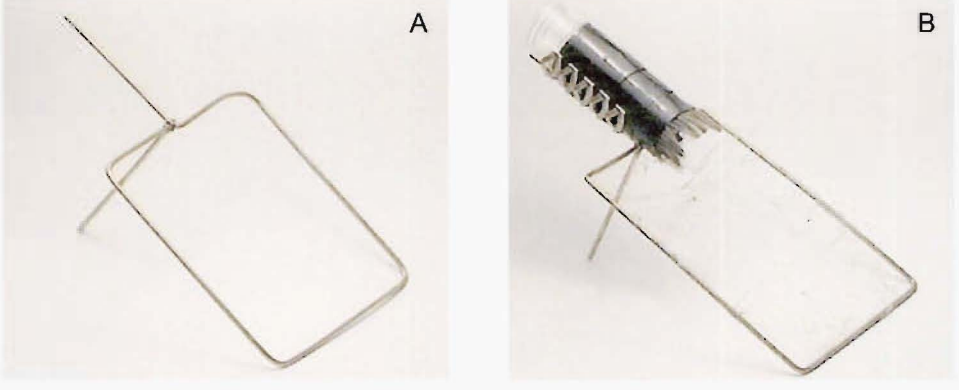


Figure 23. Web platform construction. **A.** Basic frame (welding wire tied together with copper fuse wire). **B.** Frame coated with non-sticky webbing and complete with tube for introducing *Portia.*

Presentation during tests

Experiments in Chapter 7 were based on presenting virtual lures to *Portia*. These presentations were carried out on a platform placed directly in front of the screen. This simple arrangement is all that is necessary for testing short range (e.g., within 100 mm) predatory behaviour against lures. The platform was a wire frame made by bending into shape 1.5 mm diameter brass welding wire using pliers (Fig. 23a). Layer upon layer of the sheet components of *B. longinquus* webs were then stretched over the frame. Layers were added until the silk covering had no large holes through which a *Portia* might pass. Once this was achieved, the frame was placed in a bath of 80% ethanol and left to soak for at least 10 min. *B. longinquus* is a cribellate spider. Cribellate spiders add minute cribellate fibres to large structural threads, thereby rendering their webs sticky. The stickiness assists in getting an intact layer of silk on the frame. The sticky cribellate fibres, however, are apparently dissolved by the ethanol, leaving the platform covered only by threads of non-sticky structural silk. Usually this platform held its shape, but if, during treatment with ethanol, the web covering developed holes, the process of layering on silk and washing was repeated. When finished, the platform resembles a section of a thick non-sticky sheet web. Between tests the web platform was washed again in ethanol to remove any potential chemical traces from a previous *Portia*.

Sometimes *Portia* goes into an alarmed state when transferred from its cage to the platform. Alarmed *Portia* may run across the web platform to the nearest cover or they may leap away more or less in random directions. Measures were taken to minimize alarm levels that could have confounded testing by resulting either in differences in behaviour between individuals or differences in where and how *Portia* enters the web platform. The goal was to

minimize the initial level of alarm and ensure that all *Portia* move onto the platform at more or less the same point.

Each web platform has a narrow opaque tube (internal diameter 13 mm, length 45 mm) facing the projector screen and opening onto the side of the platform opposite the screen (Fig. 23b). One end of the tube touches the web and the top and sides of this end are fringed with hair (human hair held in place by electrical tape). *Portia* is transferred from its cage into a small plastic petri dish using a small soft-tipped paintbrush to direct its movements. From the petri dish, *Portia* is transferred into the end of the tube that points away from the web. The end of the tube into which *Portia* was introduced is capped or stoppered to prevent *Portia* escaping from the reverse end of the tube (i.e., away from the webbing). In the tube, *Portia* is allowed to calm down and only then is it ready to emerge onto the web.

Before testing, it is important to check that the image of the lure is life size. For example, if the lure is of a house fly, the image of the lure on the screen should be the same size as a house fly. This calibration can be done using a micrometer to measure the body length, width and height of a dead or live specimen and comparing these measurements with those taken of the lure directly off the screen. Any necessary adjustments can be made by either re-rendering the movie files of the lure at a slightly different size or, in some cases, just adjusting the projector's zoom level.

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Chapter 3. Appendix 1 : Technical details

What follows is essentially a set of notes pertaining to specific technical issues and problems with the various components of the current VLPS. Also provided is the full code listing for the test harness program in Director 6.5.

Making lures

Bugs in Extreme 3D 2

Extreme 3D 2 has a number of bugs that occasionally affect either the program's functioning or change the appearance or structure of drawn objects. These bugs can potentially have a serious effect on a lure that is under construction. What is more, because Extreme 3D is no longer produced by Macromedia, these bugs will probably never be fixed or officially documented.

- Do not load Extreme 3D files by double-clicking on their icons in the Microsoft Windows operating system or load files using the recent documents section of the Windows start menu. Instead, always launch Extreme 3D first and then load the file using the file menu. If loaded incorrectly a bug will occur that affects all objects in the file that were created using the sweep tool. Sweep tool objects have internal ribs. The number of ribs is defined using the objects window. The bug reduces the number of ribs within all sweep objects in the file to '0', causing them to be mishapen. The only way to fix this bug is to manually redefine the number of ribs for each sweep object seperately from the object window.
- Sometimes simplified objects will suddenly appear strange and inverted. This is caused by a bug that sometimes draws the wrong side of an object first. The first attempt to fix this bug for a specific object should be to select the object, choose

the render menu and select the sides that should be displayed as either 'front' or 'both'. If this fails, try reversing the order of control points (from the objects menu). If this does not work try saving the file under a different name (for insurance), quitting Extreme 3D, restarting windows, reloading Extreme 3D and opening the file.

- Extreme 3D requires lots of memory and graphical resourses to work properly. This can cause problems when other resources hungry programs are run concurrently. For example, using CorelDraw 9 and Extreme 3D 2 together for several hours, both programs often start exhibiting unusual bugs. Typically CorelDraw will no longer refresh its own document windows. Eventually one or the other may just crash.

Other methods for creating virtual 3D objects

Virtual 3D computer graphics are now used extensively in television, books, movies and computer games. In most cases it is not expected that the human subjects of these media will be fooled by the models in the same way as it is hoped that *Portia* is fooled by lures from the VLPS. However, in some cases the aim of media is to fool the human viewer into thinking that images generated in a computer are real objects. For example, the recent movies such as 'Jurassic Park' and 'Starwars Episode 1' and the BBC documentry 'Walking with Dinosaurs' have made extensive use of virutal 3D lures that are good enough to appear real.

The typical method used in these high-budget projects typically involves using a laser based 3D scanner to trace the shape of a physical model (i.e., a clay sculpture of a dinosaur) directly into the drawing software. An almost perfectly accurate and highly realistic basic virtual 3D drawing is therefore available for the animators and graphic designers to fill in the details.

Highly accurate movement patterns for animal subjects can be defined using data taken from real animals. This is achieved by logging position data from transponders (or just white dots) placed on critical points on the animal's surface (usually joints) and applying these data directly to the corresponding points on the virtual model.

Although, these two techniques, laser scanning and using transponder data, can potentially provide more accurate results in less time than my methods, they cannot be readily applied to salticid research (yet). Expense is one reason, salticid researchers typically not having budgets comparable movie producers. However, there is a more serious physical reason; the subjects of our lures are typically too small. There is a minimum size below which laser scanning becomes ineffective because of the non-homogeneous nature of laser beams (seen as sparkles within the beam). Nor are transponders small enough to be placed on all the joints of a *Portia*-sized animal currently feasible.

Director

Macromedia Director is a powerful high-level language for writing mulitmedia programs. New versions of the package are frequently released. The version used here is 6.5. However, there is no guarantee that programs written in this version of Director will be compatable with future versions. There has been some suggestion on the Macromedia web site (http://www.macromedia.com) that future versions of the product will use code (lingo) that is more similar to, and more compliant with, the Java programming language (developed by Sun Microsystems for writing 'platform-independent' programs).

Full code for the Test Harness program

Taking advantage of Director's internal libraries and structures means that the amount of lingo used in the current test-harness program is not excessive. Like all programs in Director,

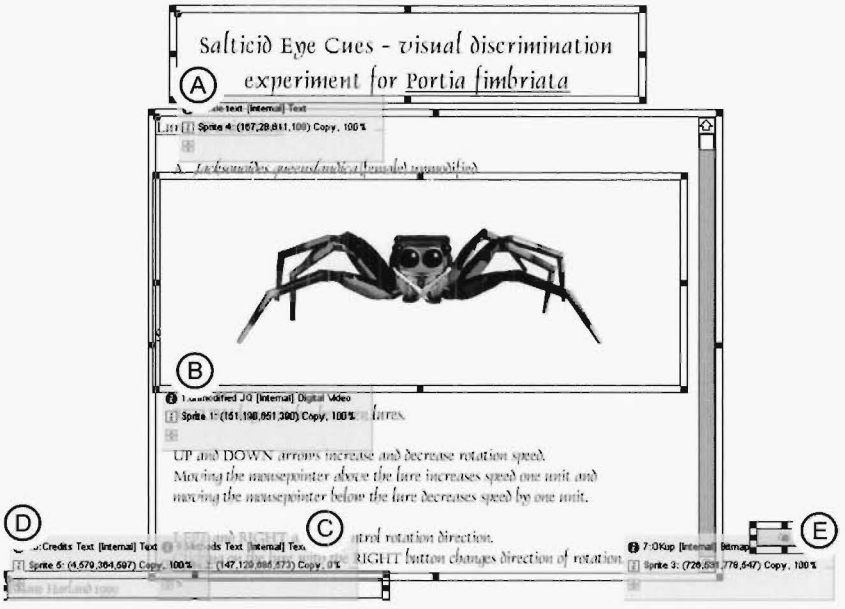

Figure 24. Sprites on the Test-Harness stage. **A**. Sprite 4, shows cast member 9. **B**. Sprite 1, shows cast member 1. **C**. Sprite 2, shows cast member 6. **D**. Sprite 5, shows cast member 10. **E**. Sprite 3, shows cast member 7.

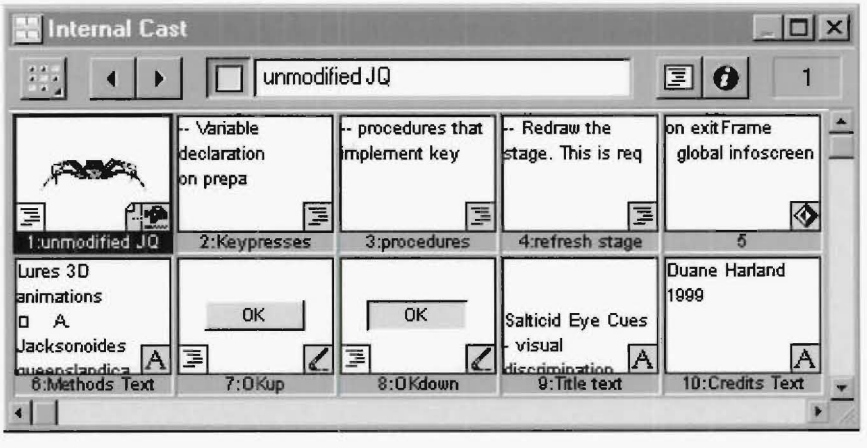

Figure 25. Test-Harness cast members. Member 1 (selected) contains lure movie and has associated code. Members 2 through 5 contain programming code. Members 6, 9 and 10 contain text. Members 7 and 8 contain bitmap pictures and have associated code.

the Test Harness is made up of cast members (arranged in a list) and sprites (arranged on a stage). Five sprites are arranged on a 800 x 600 pixel stage (Fig. 24a). Nine cast members contain lingo, text and pictures, and these can be augmented by any number of cast members containing lure movies (Fig. 24b).

Each lure member has a set of properties associated with movie file playback. Some of these settings are manipulated automatically by the lingo in the code cast member called 'key presses'. However, for best performance some must be set manually. These are:

- the file for the movie file;
- the 'direct to stage' setting (should be selected);
- the video setting (should be set to 'play every frame, no sound');
- the video rate (should be set to maximum).

Each lure member also has lingo commands that effects mouse control of lures (Code 1). If this lingo is missing the lure will respond only to commands from the keyboard (see the code for member 'key presses') .

```
on mouseDown
  if the DoubleClick then
    stopModel
  end if
end

on rightMouseDown
  if the DoubleClick then
    faceFront
  else
    changeDirection
  end if
end rightMouseDown

on mouseLeave
  if the mouseV < the locV of sprite 1 then
    increaseSpeed
  else if the mouseV > the locV of sprite 1 then
    decreaseSpeed
  end if
end mouseLeave
```

Code 1. Lingo associated with each lure cast member.

Cast member 'key presses' contains only lingo that initializes each lure cast member and handles input from the keyboard (Code 2).

```
-- Variable declaration
on prepareMovie
  global activeModel, numModels, speed, infoscreen, modelscreen,
endmodelscreen, mousevert

  set activeModel = 1
  set numModels = 1
  set speed = 0

  -- set scenes
  set infoscreen = 1
  set modelscreen = 2
  set endmodelscreen = 2

  --  prepare models
  puppetsprite 1, TRUE
  set the loop of member 1 to TRUE
  set the moveableSprite of sprite 1 to TRUE
  set the visible of sprite 1 to FALSE
  decreaseSpeed

  repeat with a=1 to numModels
    set the pausedAtStart of member a = TRUE
  end repeat

  -- handle the mouse pointer. Make it disappear when clicked
  set the mouseDownScript to "Cursor 200"
  set the mouseUpScript to "Cursor 2"
end prepareMovie
-- This procedure handles input from the keyboard
on keyDown
  global activeModel, speed
  case (the key) of
    RETURN: switchModels
    SPACE : stopModel
    "x": faceFront
    "i", "I": instructions
    "q","Q" : quit
    otherwise
      case (the keyCode) of
        123: --         left arrow
          if speed > 0 then
            changeDirection
          end if
        124: --           right arrow
          if speed < 0 then
            changeDirection
          end if
        126: --           up arrow
          increaseSpeed
       125: --          down arrow
          decreaseSpeed
       end case
  end case
end keyDown
```

Code 2. Lingo from cast member key presses. Initializes lures and handles keyboard input.

Cast member 'procedures' contains the lingo that implements switching between lures and speeding up and slowing down the playback speed of the movie files from lure members.

```
-- procedures that implement keyboard input from
-- the opperator as called from cast member 'keypresses'

-- This procedure changes the model showing by
-- cycling one model forward and reassigning the
-- variable activeModel
on switchModels
  global activeModel, numModels, speed

  -- assign a new active model. if we are at the end
  -- of the list of models go back to the start
  if activeModel = numModels then
    set activeModel = 1
  else
    set activeModel = activeModel + 1
  end if
  set the member of sprite 1 to activeModel

end switchModels

-- makes the current model play backwards
on changeDirection
  global speed
  set speed = -speed
  set the movieRate of sprite 1 to speed
end changeDirection

-- increase and decrease speed add or subtract 10%
-- from the playing speed of the current model's
-- animation.
on increaseSpeed
  global speed
  if abs(speed) > 1.9 then beep
  else if speed > 0 then set speed = speed + 0.1
  else set speed = speed - 0.1
  set the movieRate of sprite 1 to speed
end increaseSpeed

on decreaseSpeed
  global speed
  if speed > 0.09 or speed < -0.09 then
    if speed > 0 then set speed = speed - 0.1
    else if speed < 0 then set speed = speed + 0.1
  end if
  set the movieRate of sprite 1 to speed
end decreaseSpeed

on stopModel
  global speed
  set speed = 0
  set the movieRate of sprite 1 to speed
end stopModel

on faceFront
  set the movieTime of sprite 1 = 0
  stopModel
```

```
end faceFront

on instructions
  global infoscreen
  set the visible of sprite 1 to FALSE
  go to frame infoscreen
end
```

Code 3. Lingo from cast member procedures. Manipulates lure switching and lure rotation speed.

The 'refresh stage' cast member contains lingo that deals with two possible bugs in Director that can cause problems (Code 4).

```
-- Redraw the stage. This is required because large bitmaps
-- such as those used here inevitably leave some debris
-- behind when moved rapidly across the screen.

on idle
  set the stageColor to 0
end idle

-- Loop the movie.  Although this can be set in director, when
-- a projector is made it will only play the first 28 frames
-- then end. This loops back to the front of the movie if the
-- last key pressed was not "q" for quit.
-- I also find the current vertical location of the mouse here
-- to facilitate speeding up or slowing down the movie using
-- the right mouse button

on exitFrame
  global endmodelscreen, modelscreen
  if the frame = endmodelscreen then go to frame modelscreen
end
```

Code 4. Lingo from cast member refresh stage. Cleans stage of debris and loops lure playback.

Cast member "5" is associated with a specific frame in the test harness playback: frame 1. The lingo that this member contains (Code 5) loops the playback from the end of frame 1 to the beginning of frame 1, effectively halting playback on this frame (allowing the user time to read the instructions).

```
on exitFrame
  global infoscreen
  go to frame infoscreen
end
```

Code 5. Lingo from cast member 5. Halts playback on frame 1.

The remaining cast members are displayed only on the first frame of director's score. They contain instructions, title, credits, and the button that the user presses to move from the first frame (with the instructions) to the remaining frames (with the lure). The instructions, title, and credits are text cast members. Their contents depend on the specific nature of the experiment in which the test harness is used. The instructions may contain more text than will fit on a single screen. If this is the case, the 'scrolling' property must be chosen in the member's settings.

Two cast members, 'okup' and 'okdown' describe the behaviour of the 'OK' button that appears on the initial screen. Each is a bitmap cast member with associated lingo code. When a user clicks on the sprite displaying okup, its lingo changes the sprite's cast member to okdown (Code 6). Okdown simply breaks out of the loop imposed by cast member 5 by moving to the next frame and making the lure visible (Code 7).

```
on mouseDown
  set the member of sprite 3 to "OKdown"
end
```

Code 6. Lingo associated with member okup. Changes clicked sprite to okdown.

```
on mouseUP
  global modelscreen, speed
  go to frame modelscreen
  set the visible of sprite 1 to TRUE
end
```

Code 7. Lingo associated with member okdown. Changes to next frame (exits initial screen) and shows lure.

The score (Fig. 26) defines when sprites appear on the stage (i.e., frame in the director movie in which sprites and events occur). The stage for the basic test harness has a score with two active frames. The activated program is always looping endlessly in one of the two frames: the first frame (initial screen containing instructions, etc.) (Fig. 26a) or the second frame where only the lure sprite is active (Fig. 26b). Pressing the 'i' key on the keyboard and pushing the ok button on the initial screen switches between the two loops.

Suggestions for future modifications

The VLPS is a powerful tool. The current set up and experiments have only just scratched the surface of what is possible using this technology to investigate perception and behaviour in *Portia* and other salticids. The Test Harness program is one of the places where changes will almost certainly be necessary when adapting the VLPS to new experimental designs. The following examples outline a few of the possible expansions that might be made to improve the current test harness or adapt the current test harness for new types of experiments.

The current test harness was designed to provide a high level of continuous interactivity between the researcher and *Portia.* The lure is under continuous control of the researcher. However, this is not always desirable because for some tests more control of a lure by the researcher can mean more inter-test variability in presentation, thereby introducing risks of error and subjectivity.

The aim of tests in Chapter 7 was first to get *Portia* to stalk the lure (*Portia* that did not stalk the lure were not counted) and then to test *Portia*'s reaction to a few specific manipulations of the lure. The time taken for *Portia* to begin stalking was highly variable and depended on the individual being tested; therefore, a high level of interaction during this initial stage was best. Once *Portia* began stalking, further manipulations of the lure had to be presented in a highly standardized manner.

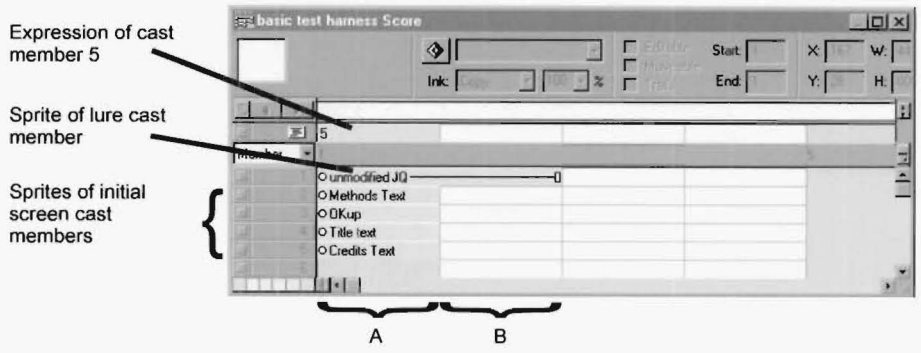

Figure 26. Score of test harness in Director showing sprites active on different frames. **A**. Initial screen; frame 1. **B**. Lure presentation screen; frame 2.

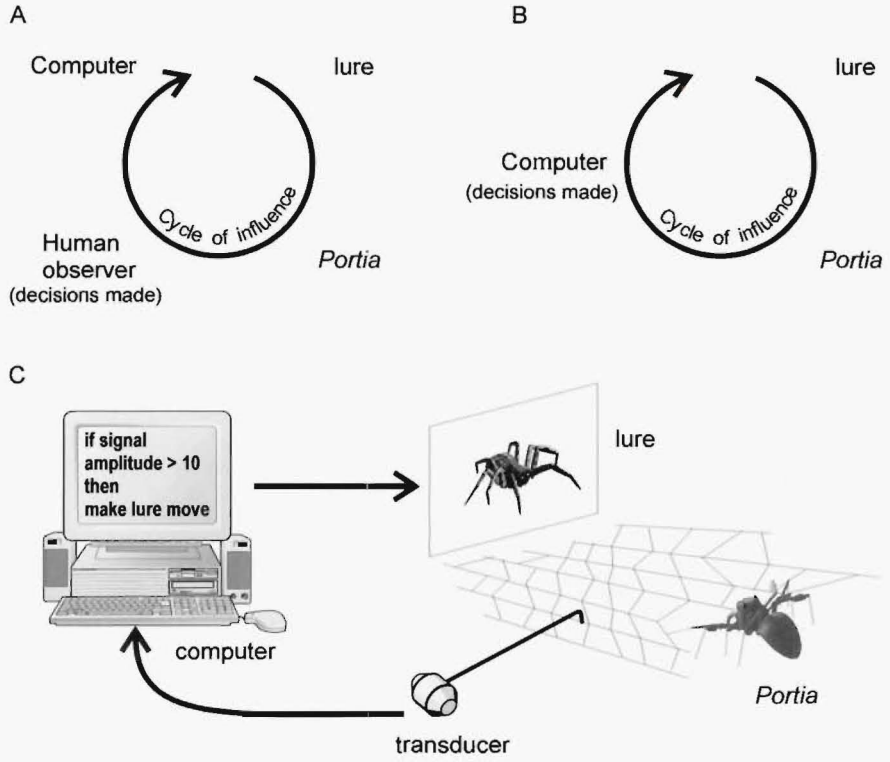

Figure 27. Two forms of interactive test harness. **A**. *Portia* interacts with lure through researcher and computer. **B**. *Portia* interacts with lure directly with computer. **C**. Example interaction loop. *Portia* interacts with lure. Web signals picked up by transducer arm and ported into computer. Computer implements decision algorithm and appropriately manipulates lure. Lure behaviour may influence *Portia* and so on.

A simple example of standardizing lure movements also comes from Chapter 7. After stalking began, *Portia* was tested to see if it would freeze when suddenly faced by the lure. Instead of rotating the lure around to face *Portia* in individual steps (i.e., first facing the lure away, speeding up the lure's rotation and then rapidly slowing it when correctly oriented), a single step was applied which instantly rotated the lure from its present orientation to facing forwards. Substituting actions that would normally require several steps with a single command helps to standardize tests. However, much more is possible. For example, automating the lure to suddenly face *Portia* could be further standardized by having a single sequence that initially turns the lure away, freezes it for a moment and then rapidly turns it to face forwards. This one sequence could be triggered by a single key on the keyboard or could be triggered at some specific time after stalking commences.

At the most extreme, a lure's movement patterns could be defined as a set of pre-programmed automated sequences that are triggered by the researcher using different keys or are set to occur at different times without input from the researcher at all. Pre-set sequences could each be defined by a different animated movie file from Extreme 3D and the test harness could be used for switching between them (see Code 2 & 3). Alternately, sequences of movement patterns could be defined in director for specific sprites and isolated from each other in time using the score. Switching between sequences could be achieved by jumping to different frame numbers within the score (e.g., first lure manoeuver, frames 1-30; second lure manoeuver, frames 31-40).

Besides presenting a single lure (represented by a single sprite in director), multiple sprites might be used to present multiple lures concurrently. Each lure that is presented simultaneously could display independent pre-set movement and behaviour, or all lures might be linked to a single interactive set of controls (e.g., one key might cause all lures to start to rotate, another key might cause all to stop, etc.)

Interactivity has so far been described only in terms of a human researcher watching *Portia*'s reaction to the lure and responding by manipulating the lure's behaviour appropriately (Fig. 27a). Given a high level of standardization of movement patterns, experiments would be possible with the human removed from the interactive loop, letting *Portia* interact directly with the test harness program (Fig. 27b).

An example of an experiment where *Portia* might interact directly with the computer is illustrated in Fig. 27c. Such an experiment might be set up to test hypotheses about aggressive mimicry during web invasion. Web signals could be imported into the computer through an analogue-digital converter and analysed to isolate a specific feature of the signal. The computer could then provide a pre-programmed response by the lure, depending on the feature's quality.

Display system

Any system made up of multiple parts will typically have one weak link in the chain that reduces the power of all other components to that level. The display system for converting computer output into something that the salticid can see is, and probably always will be, the weak link in the VLPS. Of all the parts of the current system, the projector took the longest time to get working and tuned.

Computer projectors have three basic components (Fig. 28). A bulb provides a constant supply of light. The light from the bulb is condensed, collimated and sometimes filtered to remove the UV and IR components. Between one and three liquid crystal pixel arrays augmented with coloured filters introduce the picture from the computer into the light path. A final set of lenses focuses an image of the pixel arrays onto a screen at some distance in front of the projector. Commercially available projectors are not designed with spider audiences in mind. Most will have lenses that can not focus an image any closer than about a

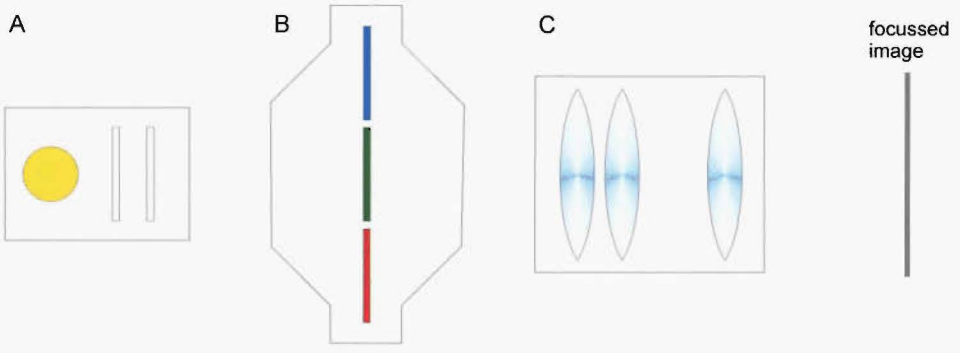

Figure 28. Basic components of an LCD computer projector. **A**. Bulb, diffuser, condensing lenses and UV or IR filters. **B**. Red, green and blue filtered LCD arrays. Light may be split up, passed through each array then combined back together into single path. **C**. Primary lens array. Image of LCD arrays is focussed somewhere in front of projector.

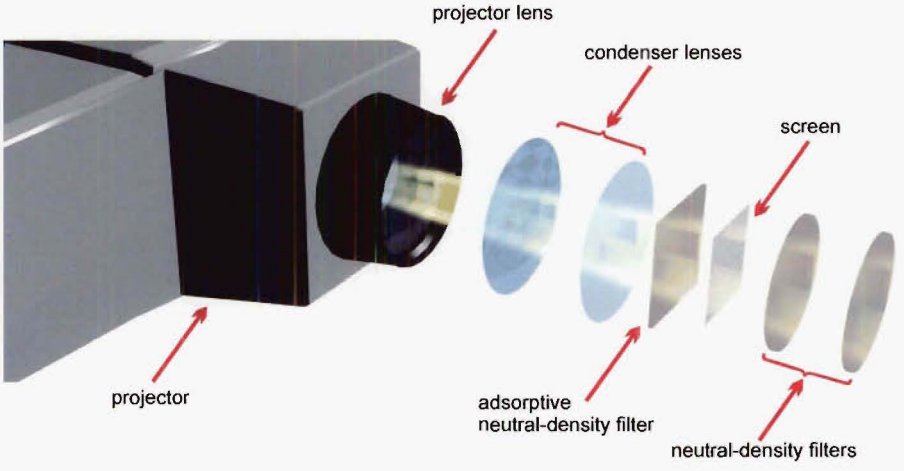

Figure 29. Exploded view of lens array components. Light from projector is focussed by projector lens. Focus adjusted by condenser lens set. Intensity reduced by absorptive neutral-density filter (spectral properties maintained and no light reflected back at projector). Image focussed on screen. Final set of neutral-density filters increase contrast of image on screen. To scale, but components more closely spaced than pictured.

metre from the projector (i.e., minimum image size is still too large for *Portia*). What is more, the image brightness, contrast and colour range is designed specifically with only human audiences in mind.

Depending on the model of projector, it may be possible to compensate for some shortcomings by making adjustments to the light source, filters and lens. First, the image must be reduced in size so that lures are a realistic size and have a high enough resolution (in terms of pixels per area) that they are displayed clearly.

Replacing the lens

If the projector is of a sort that allows the lens to be removed without doing damage to the rest of the unit, then replacing the original lens is the simplest way to achieve good image reduction. A quick and effective replacement is to use a ready made lens, such as a lens from a SLR camera (as long as the aperture is wide enough). An especially good idea comes from Phil Taylor and David Clark (Phil Taylor, pers. comm.): using a zoom lens from a SLR camera (placed backwards in the light path) allows the projected image to be easily sized using the lens zoom function.

Replacement lenses may also have an adjustable iris (or diaphragm) that could be used to reduce unwanted brightness from the image. However, an adjustable iris may cause the same problems as does a standard neutral-density filter (see below).

Lens array

In some cases, (including in the case of the projector I used) it is not possible to remove the projector's existing lens without causing irreparable damage to the projector, or causing it to stop functioning at all. An alternative is to augment the existing lens array with additional lenses that reduce the image (Fig. 29; 30). One advantage of an external lens array is that the focus and zoom functions of the projector's own lens can still be used.

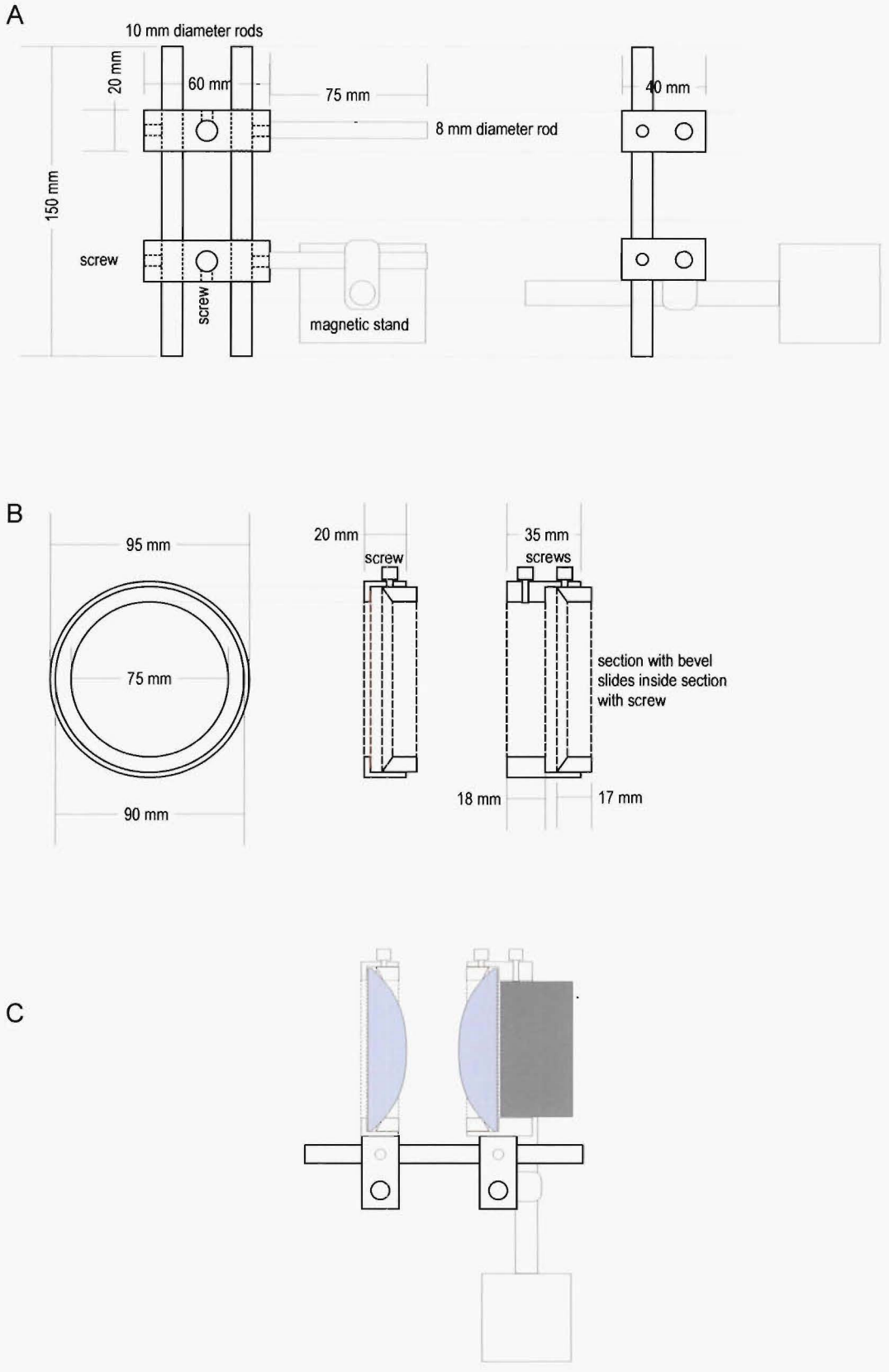

Figure 30. Blueprint of lens array. **A**. support frame, top (**left**) and side (**right**) views. **B**. lens and filter holders. Designed to take 900 mm diameter uni-convex condensing lenses and 72 mm diameter photographic filters. **C**. Longitudinal section (side view) through finished lens array, two condensing lenses (blue) and block of filters (grey) are in place.

The current lens array is made up of a set of 90 mm diameter reducing lenses each with a focal length of approximately 120 mm. The lenses are positioned close together with their round sides almost touching and simply act to adjust the plane of focus of the projector's original lens array. Images from the projector are therefore brought into focus a few centimetres in front of the projector, rather than at many metres away.

Reducing image intensity

Reducing the size of a projected image results in an increase in image intensity. There are many potential methods of reducing the image brightness. The most obvious would be to reduce the brightness of the projector's light source (i.e., the bulb) by filtering the light using neutral density filters or an adjustable iris (perhaps between the condensing/collimating lenses). Turning down the light intensity of the bulb itself (i.e., dimming) is probably not an ideal solution because the spectral output of the bulb may change (typically it gets more yellow when operating dimmer).

Another solution is to reduce the image intensity at the projector's lens or lens array. This can be done in three ways.

- Darkened filters can be used to reduce the light level. Neutral-density filters are best because they reduce brightness evenly over the visible spectrum. This means that the spectral properties of the light will be unchanged. Typical neutral-density filters work by absorbing some light and reflecting some light back along the optical axis. There is a small danger (especially with long exposure) that light reflected back into the projector may cause damage to the LCD arrays and contribute to problems of overheating. However, special absorptive neutral-density filters that reflect minimally are available.

- Using an adjustable iris to reduce light levels is also effective if it placed correctly within the lens or lens array (any SLR camera lens used will have a built-in adjustable iris). However, an adjustable iris suffers from the same problem as the neutral density filters. Unless the surface is coated with a neutrally absorbent material (e.g., mat black paint) a significant amount of light will be reflected back through the projector (more so even than with glass filters).
- Using beam splitters (e.g., partially-silvered mirrors) is one method of reducing light levels without the danger of reflecting light back into the projector. A beam splitter can be placed between the projector's existing lens and the lens array, and angled at 45° to the optic axis to direct some proportion of the light away at right angles. However, beam splitters can introduce their own problems. First, the splitter takes up much more space than a filter or iris. Second, if the light that is split off from the axis is directed at a reflective surface, some may be reflected back into the system, especially if the splitter is inside a metal container. Third, beam splitters are typically made of glass. Most light will be reflected off the silvered side of the glass, but some will also be reflected off the non-silvered side. Depending on the set up, this can result in a faint double-image.

The current lens array uses only neutral density filters to reduce image intensity. Multiple filters are stacked together to form a block. Ideally only one filter should be used, but using multiple filters can provide better fine control over exact brightness levels. The two filters closest to the projector within the block are neutral density filters. These are designed to absorb maximally and to reflect light minimally.

The current lens-array system is a pair of condensing (or reducing) lenses. Condensing lenses have only one curved surface, the other being flat. The two curved surfaces are positioned to face one another so that they are almost touching. Having flat surfaces on the

outside is convenient when experimenting with lens set ups and applying different filters. However, condensing lenses are not ideal for a final product. A disadvantage of the condensing lenses is that they must be much larger than the image because of severe spherical aberration effects from their edges. Chromatic aberration is also a factor. An alternative way to increase image quality might be by using spherically corrected, coated, achromatic lenses. What is more, the lens diameter would not need to exceed the image size by such a large margin. The downside to using achromatic lenses is that they are typically expensive, especially if they also correct chromatic aberration in both the visible and UV regions of the spectrum (salticids can detect light of shorter wavelengths than can humans).

The final part of the lens array (or replacement lens) is the screen. Typically the quality of the screen is the main factor that limits the quality of the projected image. For normal projection (i.e., the viewer sits behind the projector or in between projector and the screen), the graininess of the screen usually does not have much impact on the quality of the focussed image. However, when the image is back-projected on to a screen (i.e., when screen is between projector and viewer), screen graininess and thickness are critical factors controlling image quality.

For back-projected images the ideal screen would be thin and opaque, it would have a grain size as small as possible and it would be neutral grey in shade. After years of searching my impression is that such a screen may not exist. The closest to ideal I have so far found are various forms of fine-grain technical drawing plastic. Thinness and grain size are the most important factors. If a material is too thick (i.e., any thicker than a standard sheet of paper), images projected on it will appear very fuzzy because the light from any in-focus image on the far side of the screen must travel through the screen to be seen. The thicker the screen, the more diffusion occurs. Grain size is also important. It is grain size that will determine the

resolution of an in-focus image. If the grain is too large it is clearly visible overlaying the picture.

The drawing plastic that is used as a screen in the current lens array is white in colour. Consequently the parts of the image that are black (i.e., no light projected onto that region) appear the same colour as the screen (i.e., white). To us, these regions appear black because, in our minds, we compare them with the much brighter white or coloured regions. What a *Portia* might see is less clear. To overcome this potential problem, a second series of neutral density filters is placed in front of the screen to increase image contrast.

Spectral output and colours

The light produced by any device that is used to present computer-generated lures to salticids will have a spectral profile. Some wavelengths of light will be outputted more intensely than others. Certain regions of the spectrum may not be outputted at all. Computer output devices (e.g., monitors, projectors etc.) have had their spectral profiles carefully chosen and tuned to allow reproduction of colours that look accurate to human viewers. The designers of these devices did not have salticids in mind, and this can potentially lead to problems if the researcher does not understand how the visual system of salticids (especially colour vision) works.

The receptors in salticid eyes and those in our own are almost surely different in their sensitivities to any particular wavelength of light. A coloured object to which a salticid responds (e.g., bright blue stripes on a conspecific) might be reproduced on the computer and projected so that, to us, the colour of the original object and the virtual object are identical (e.g., both the lure's and the virtual lure's stripes may appear to us to be exactly the same shade of blue). However, to a salticid, the real object and virtual object may appear quite different. Salticids tend to be sensitive primarily to wavelengths of light between UV and

green (Blest et al. 1981) and less sensitive to wavelengths longer than green, but knowing this alone is not enough if we want to match colours that we see with the "colours" that a salticid might see.

The simplest solution is to not carry out experiments using colour. Experiments where colour is not important can still be done so long as the spectral output of white light produced by the projector adequately covers the range of wavelengths to which the photo-receptors in layer I of the salticid AM eyes are sensitive (Fig. 31). Even then, some unknown use of colour cues may influence the salticid's behaviour. For my experiments all virtual lures were presented to *Portia* in grey scale. The lower stalking tendency of *Portia* to virtual lures compared with dead lures (e.g., see above section on effectiveness of VLPS) might be a caused by colour errors.

This warning notwithstanding, experiments that use a VLPS system to investigate colour cues should not be completely ruled out. A computer LCD projector can potentially be tuned to the spectral sensitivity profile of a salticid's visual system, but it would be a somewhat involved process. It may, in fact, not be worth the trouble.

- An accurate spectral sensitivity profile would be required for the principal and secondary eyes of the salticid to be investigated.
- The spectral output profile of the unshielded projector bulb would have to cover the range of the salticid's sensitivity profile.
- A UV filter would have to be installed to cut off wavelengths lower than those that occur in the salticid's sensitivity profile (as these may be dangerous to both salticids and humans).
- Red, green and blue filters should be removed from the LCD arrays and replaced. The replacement filters (e.g., green, blue and UV) should produce a spectrum that is as similar as possible to the salticid's sensitivity profile.

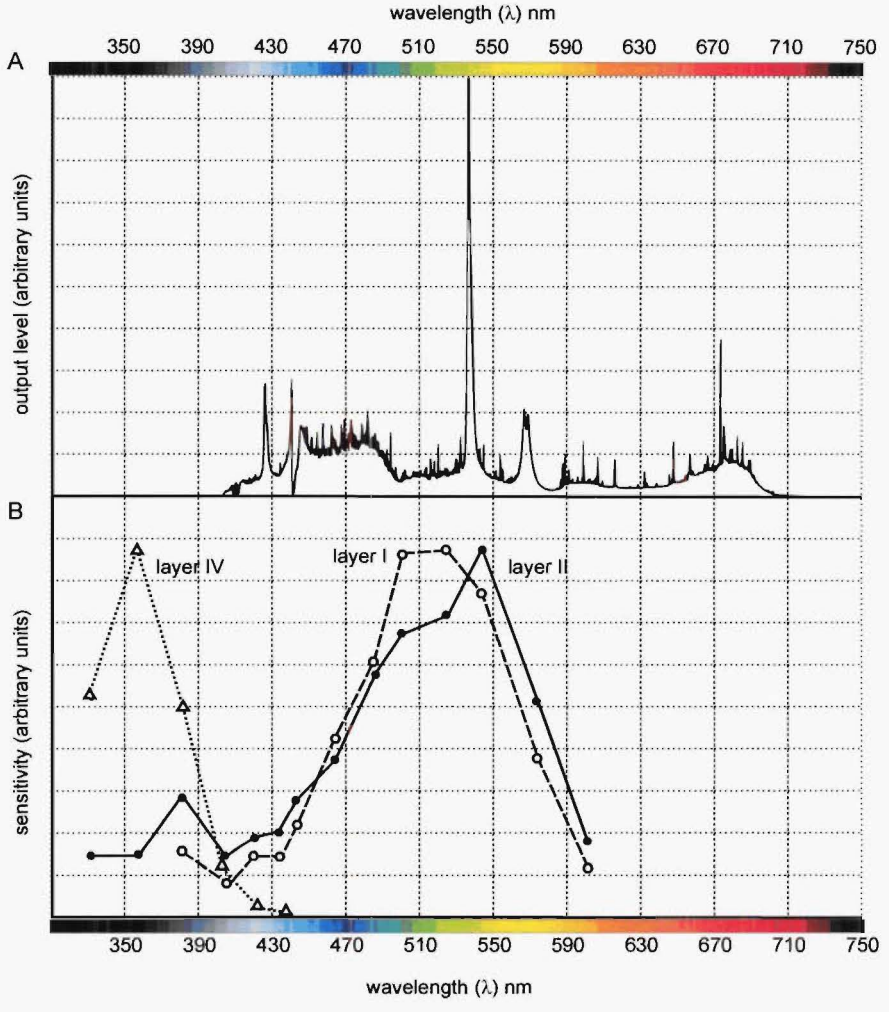

Figure 31. Spectral output of projector and spectral sensitivity salticid vision. **A**. Spectral output of white light from Telex P400 LCD projector. **B**. Spectral sensitivity of marked cells from layers IV, II and I within the AM eye of *Plexippus validus* (after Blest et al. 1981). Note; projector's output does not cover that region of the spectrum to which layer IV is especially sensitive.

- The lenses within the projector would need to tested for unwanted chromatic aberrations (e.g., of the filtered UV light).
- Having tuned the projector to the salticid's sensitivity profile, coloured objects could be reproduced as virtual lures by using a spectrograph to get a reflected colour profile from the original object and then colouring the virtual object so that the output profile for that colour from the projector is the same (when measured with the spectrograph).

Alternative ways of presenting images to salticids

In this thesis virtual lures were presented to *Portia* and other salticids only on simple platforms, but presentation of lures need not be restricted to platforms alone. The screen could be placed at the edge of a real web, or in a cage or box. The only danger is that chambers that have the screen at one end may cause problems if the screen can be reflected off the walls, floor and ceiling. Glossy flat walls in a chamber might present a salticid with multiple images of the screen. Before testing, chambers should be inspected for unwanted reflections at salticid-eye level.

In the current set up, images of lures are back-projected onto a screen. However, projected lures can also be forward-projected onto a screen or other object, and just about anything could be used as a screen (e.g., screen in a web, on a tree trunk, on a dead lure etc.). Mirrors or fibre-optic image conduits could also be used to place the image into areas where the projector will not fit.

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Chapter 3. Appendix 2: Development History

Here I give a brief account of the process by which the current VLPS was developed. This documents some of the critical steps in my research and acknowledges people who provided vital ideas.

Presentation system

The basic idea for a presentation system for displaying virtual prey to salticids arose because of a discovery by David Clark (Alma College, State of Michigan, United States of North America) (Clark & Uetz 1990) that *Mavia inclemens,* an insectivorous salticid from North America, will respond to footage of prey and conspecifics presented on a small TV set. Further work (Clark & Uetz 1992, 1993) on the mating strategy of *M. inclemens* expanded on the initial study, they used rudimentary computer-animated virtual lures captured from video playback. By today's standards, Clark and Uetz's virtual lure system was crude, but at the time it was pushing the limits of what was possible with the computer technology then available. To me, in 1996, this earlier work suggested an enormous potential, and formed a starting point in my own development process.

Development of the VLPS was in essence the development of new technology, and like most scientific research it is never straight forwards. Much of the development process involved trail-and-error learning as I experimented with different ideas and arrangements of components. My initial task was to replicate for *Portia* the kind of tests first tried by David Clark with *M. inclemens*. There was no guarantee that *Portia* would respond to a TV as well as *M. inclemens*, or at all. After all there are good reasons (Chapter 2) to suspect that *Portia* possesses more complex perceptual mechanisms than most insectivorous salticids.

The first test was finding out how a mature *Portia* female would react when presented with another mature female that was displaying. Video footage of a female *P. fimbriata* was

captured from the front using a mirror (Fig. 32a) and played back to other female *P. fimbriata* on a small LCD TV set (Fig. 32b). Of the first eight mature females tested, five oriented at the video image and two displayed, at least briefly, as they would to a mirror image. That any *P. fimbriata* would respond at all was encouraging, but it still had to be established that they were responding to the image on the TV and not, for example, the TV's flickering or even their own reflections in the screen.

A second test used a small CRT screen (the eye piece from a video camera). In this test the aim was to compare *P. africana*'s responses to video footage of a small black web spider and video footage of a similar sized black dot. My prediction was that *P. africana* would stalk only the former. At the start of each test, *P. africana* was allowed to watch the footage for a few minutes from behind a transparent barrier (Fig. 33). The barrier was then removed and *P. africana* could approach the screen. A mirror at 45° to the TV set ensured that *P. africana* could not see its own image reflected from the screen. When the footage was of a spider, *P. africana* tended to stalk towards the part of the screen with the spider. When the footage was of a spider-sized black dot, instead of stalking *P. africana* tended sit still or wander around, only infrequently moving towards the screen. I now had evidence that, not only could *Portia* discriminate between image content ($N = 40$; test of independence, chi-square; $P < 0.005$), but also that it would direct reactions for an extended period towards a video playback of prey.

Small TVs, whether LCD or CRT, had severe limitations for presenting virtual lures. Foremost was the problem that small TVs typically had poor image resolution (the LCD screen being only 300x200 pixels) and they provided an unacceptable level of flicker that could potentially interfere with experiments. What was needed was a more flexible method of presenting lures. A steady light source was needed, and a system was needed both for scaling down and for adjusting resolution. Something like a slide projector was considered.

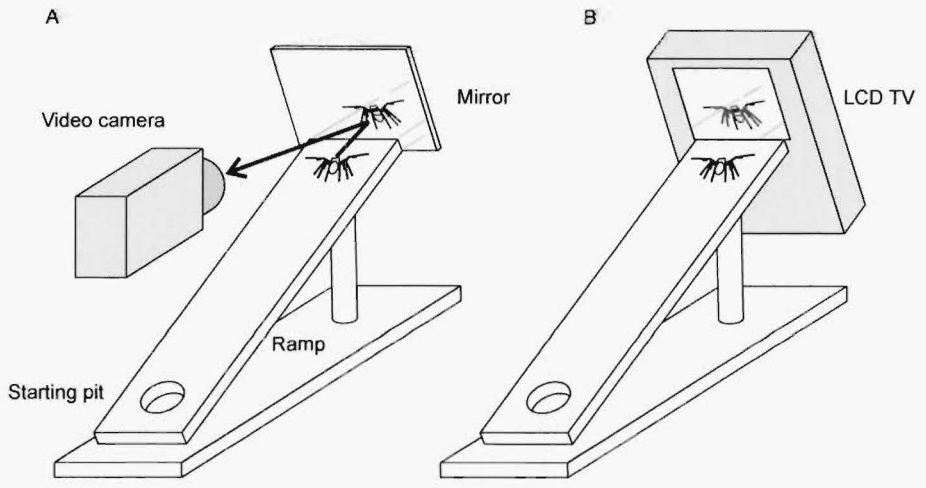

Figure 32. Set up for displaying video footage of a conspecific to *Portia*. **A**. Video taping of frontal view of female *Portia* displaying to mirror image. Mirror is angled slightly away from perpendicular with ramp to prevent live spider obscuring part of mirror image. **B**. Video playback presented to *Portia*'s on a small LCD TVset.

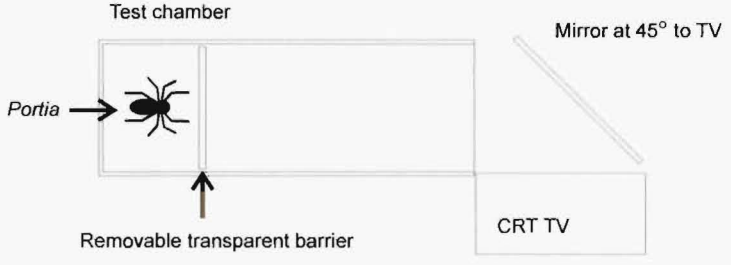

Figure 33. Set up for displaying a video prey to *P. africana* on a CRT screen. *Portia* sees reflection of screen in mirror through transparent barrier. After 2 minutes, barrier removed and *Portia*'s behaviour is observed.

At that time the modern type of computer projector was not available, or even known of, in New Zealand. LCD-OHP projection panels were considered, but then came serendipity.

In May 1996, I visited my friend Isaac Freeman in his new flat. In the most recent issue of Wired magazine (which lay open on his bed) was an advert for a computer projector. The projector seemed more-or-less perfect for my purposes. However, it was another year before money became available to buy one.

Once the projector was bought, there was the problem of reducing the image to an appropriate size. My first idea was to replace the existing projector lens, but on opening the case I was confronted with what appeared to be a solid block of electronics. Removing the lens would not be possible without virtually destroying the projector. I went to plan B and designed an external lens array (built by Nick Etheridge; Department of Zoology, University of Canterbury) to reduce the size and intensity of the image.

Initially there was no screen. A perfect image of the LCD arrays was focussed on a point in mid air just forward of the external lens array. However, discussions with Dr. David Blest (Research School of Biological Science, Australia National University, Australian Capital Territory, Australia; retired) revealed the possibility that such a system might produce confounding effects when viewed by *Portia* (because of the structure of the salticid AM eyes). Consequently I added a fine screen of drafting plastic. The final touch was to manipulate the number and position of the different neutral-density filters in the lens array to increase the image contrast to an optimum level. Getting the contrast just right was tricky and time consuming, but by late 1998 the salticid movie theatre was open for business.

Clark and Uetz had used in their studies video footage (1990) and simple animations made directly from small sequences of captured video footage (1993). For the purposes of investigating brief periods of natural movement (e.g., courtship displays), using animated sequences modified from captured video footage was both effective and relatively easy. However, using video footage can present serious limitations when asking questions about the specific features that provide visual cues (i.e., removing specific features that might provide visual cues), and also for experiments in which it is necessary for the researcher to have fine control over the lure's behaviour. Producing a video clip in which a live lure is moving in exactly the desired manner can be extremely difficult. Building a looped sequence of video with the desired movement pattern in which some parts of the prey have been removed (e.g., the first and third legs) or have been replaced with parts from another lure (e.g., a house fly leg) may be close to impossible.

From the beginning I realised that video capture imposed unacceptable limitations for producing the kind of virtual lures required for controlled experiments on visual cues used by *Portia*. Virtual 3D drawings seemed to be the best alternative. Lack of funds prevented me buying the most suitable computer for designing 3D lures, but in 1997 I finally acquired a cheaper alternative computer that met with my absolute minimum requirements.

Like research itself, development of the VLPS had periods of advancement and periods of severe set backs. The biggest set back (other than shortage of funds) during the development process was a poor choice of subject for my prototype series of lures. I had begun the development process by presenting adult *Portia* females with video of a displaying rival (Fig. 32b) and I decided to replicate this set up using 3D virtual lures. I constructed lures of an adult *Portia* female. During the construction of this lure most of the techniques

for building virtual lures (described in this chapter) were developed. However, when tested with real *Portia*, a mixture of poor screen contrast and presumably missing essential cues on this prototype lure meant that few *Portia* responded and less than 10% gave an appropriate or prolonged response. Six months to a year were spent struggling to achieve acceptable results with this lure. In 1998 I changed tack and presented new lures to *Portia*. Unlike the prototype lure, the new lures were of prey. *Portia* more readily stalked virtual lures of spider prey, and insectivorous salticids reacted even more vigorously to virtual insect prey than did *Portia* to virtual spider prey.

The final VLPS system

The final product came together during a period of research with Dr. Stimson Wilcox at his lab in the University of Binghamton (New York State; United States of North America). With help from Dr. Wilcox (who introduced me to a throng of tricky testing tactics like the tube fringed with hair etc.) and the use of his computer/video editing equipment and small TV projectors (it was easier to modify these quickly than the projector back in NZ), I was able to quickly establish the contrast settings necessary to project virtual lures. It was also in Dr. Wilcox's lab that the first version of the Test Harness program and the washable web-platform was developed.

When I arrived back in New Zealand I was able to start immediately on *Portia* perception experiments using the finished VLPS system.

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Distances at which jumping spiders (Araneae: Salticidae) distinguish between prey and conspecific rivals

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Abstract

Distances at which jumping spiders (Salticidae) use optical cues to distinguish between prey insects and conspecific rivals were investigated using adult males of 37 species. During tests, salticids walked up a ramp toward a mirror or toward an insect enclosed in a transparent petri dish. All species directed threat displays toward their own mirror images and the displays were comparable to each species' typical behaviour during male–male interactions. The salticids never displayed in tests with insects at the top of the ramp. The virtual distances at which the spiders displayed are interpreted as an indication of the distances at which each species can distinguish rivals from prey. Representative species were from the subfamilies Lyssomaninae, Spartaeinae and Salticinae. Discrimination distances relate well to the foveal layer I receptor mosaics of the anterior median eyes for the three subfamilies. Compared with the salticines, the lyssomanines and, except for *Portia,* the spartaeines tended to have shorter discrimination distances. *Portia* spp. had discrimination distances comparable to the longest recorded for the salticines. The longest discrimination distances found were for the salticine *Mogrus neglectus* (max. 320 mm or 42 body lengths) and for the spartaeine *Portia fimbriata* (280 mm or 47 body lengths).

Key words: jumping spiders, Salticidae, visual discriminations, principal eye

INTRODUCTION

Jumping spiders (Salticidae) have eyes with spatial acuity that exceeds by a wide margin that known for other spiders (Land, 1969*a*,*b*, 1985; Blest, McIntyre, & Carter, 1988). Of a salticid's eight eyes, the more laterally positioned anterio-lateral (AL), postero-medial (PM), and postero-lateral (PL) eyes, called collectively the 'secondary eyes', function primarily as movement detectors and have only modest acuity (Land, 1971; Duelli, 1978; Forster, 1979). However, two large forward-facing anterior median (AM) eyes (the 'principal eyes') are structurally unique and support visual acuities with no known parallels in any other animals of comparable size (Williams & McIntyre, 1980; Blest, Hardie *et al.*, 1981; Land, 1985).

We present comparative data on 'discrimination distances', defined as the distance at which a salticid discriminates using optical cues alone between another salticid ('rival') and an insect of comparable size ('prey'). We consider: (1) how prevalent long discrimination distances are among salticids and (2) whether the taxonomically primitive subfamilies Lyssomaninae and Spartaeinae, with inferior AM foveal layer I sampling mosaics, have relatively short discrimination distances.

The Lyssomaninae and Spartaeinae are regarded as groups that branched off early from the salticid stock (Wanless, 1980, 1984; Jackson & Pollard, 1996). However, subfamily placement for the majority of salticids is ill defined. We follow Chickering (1946) and refer to all salticids other than the Lyssomaninae and Spartaeinae as Salticinae.

Previous information on discrimination distances has been mostly anecdotal. Drees (1952) concluded that salticids have discrimination distances of 5–10 body lengths, but other studies suggest that longer distances may be common. For the genera *Evarcha* and *Salticus* (5–8 mm body length), Homann (1928) and Heil (1936) demonstrated that spiders begin stalking when they see house flies or other prey-size objects (e.g. Plasticene pellets) as far as 170 mm away. By using motionless models made from dead salticids in lifelike postures, Heil (1936) investigated the distances at which *Evarcha* initiate the courtship and threat displays normally used in interactions with conspecifics. He observed displays from *Evarcha* males at distances of up to 150 mm away. Even greater discrimination distances are suggested by observations of the males of *Trite planiceps* (body length 10 mm) and *Phidippus johnsoni* (body length 9 mm) displaying at living conspecifics from distances of, respectively, 200 mm and 500 mm (Forster, 1979; Jackson, 1980).

In an experimental study of *Portia fimbriata*, a spartaeine, and *Jacksonoides queenslandica* (formerly *Lagnus* sp.), a salticine, non-optical cues were eliminated by placing prey behind glass and using a mirror to simulate a rival (Jackson & Blest, 1982). These spiders displayed to their own mirror images from virtual distances (double the real distance from spider to mirror) up to 270 mm (*P. fimbriata*) and 330 mm (*J. queenslandica*) away, but stalked when presented with prey behind glass at comparable distances. Here, our testing procedure is comparable to that of the earlier study (Jackson & Blest, 1982).

MATERIALS AND METHODS

Cage design, maintenance procedures, terminology, and basic testing methods were as in other studies of salticids (Jackson & Blest, 1982; Jackson & Hallas, 1986*a*) and only essential details are given here.

Each test was carried out between 09:00 and 17:00 (laboratory light regime, 12L:12D; lights on 08:00). Before testing, salticids were fed *ad libitum*, then held without prey for 3-5 days. As salticid females tend to be less inclined than males to display at conspecifics (Jackson & Pollard, 1997), only mature males were used. An individual salticid was tested only once.

The apparatus was a 320 mm long wooden ramp (70 mm wide, 17 mm thick) inclined at 20° to horizontal, with either a mirror or a glass petri dish containing prey positioned at the top end (Fig. 1). The ramp, supported by 2 wooden poles glued to a wooden base, was covered with a transparent plastic overlay on which distances from the top were ruled at 5-mm intervals. Between tests, the overlay was cleaned using water and ethanol, as were any wood surfaces of the apparatus touched by a spider in a previous test. Lighting was from a 100 W tungsten filament lamp bulb, positioned 1 m above the ramp and by fluorescent tube ceiling lights 2 m above the ramp.

Before each test, a salticid was placed in a pit (diameter 32 mm, centred 65 mm from the bottom of the ramp) drilled through the plastic overlay and into the top surface of the ramp. The pit was covered by a piece of glass until a spider became quiescent, then uncovered to start the test. Salticids tend to walk up inclines and the angle of the ramp was sufficient to ensure that a spider usually ascended toward the mirror or petri dish.

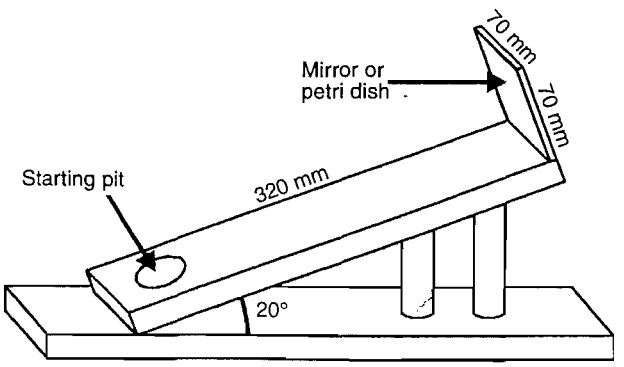

Fig. 1. Testing ramp. Salticid emerges from pit at base and ascends toward mirror. For each test, a clean plastic overlay was placed over a 5-mm grid on the ramp.

The mirror (70 × 70 mm) at the top of the ramp was positioned perpendicular to the incline so that a spider could see its own reflection when walking up the ramp. When a salticid displayed for the first time, the distance between the mirror and the anterior margin of its cephalothorax was recorded. Being interested only in the initial display distance for each salticid, distances of subsequent displays, duration of displaying and other features of interactions with the mirror were not recorded. We ignored trials with mirrors during which spiders failed to display because motivational factors did not concern us. The distance recorded from mirror tests was the real distance from spider to mirror combined with that of the virtual image from the mirror. That is, spider to mirror distances were doubled.

Ramps with petri dishes had, instead of a mirror, a 70 × 70 mm brown block of wood with a clear glass petri dish (60 mm diameter) positioned in a 60 mm diameter pit cut into the wood. Four flies of the same species were put inside the petri dish. Throughout all trials the flies moved about actively in the petri dish. We chose flies that were comparable to the salticids in body length (*Drosophila melanogaster* (Meigen), 2–3 mm; *D. immigrans* (Sturtevant), 3–4 mm; *Musca domestica* (L.), 7–8 mm; *Calliphora vicinea* (Robineux-Desvoidy), 10 mm).

Tests with insects in the petri dish were controls. We accepted an initial display distance as an indication of an individual salticid's discrimination ability only if that individual failed to display at insects comparable to itself in body length at all distances between the display distance from the test with the mirror and test with the petri dish. For each species, an individual was assigned at random to 1 of 2 groups: group A, tested with insects before testing with the mirror; group B, vice-versa.

All tests ended when a salticid left the ramp, went underneath the ramp or reached the top of the ramp (i.e. touched the mirror or the petri dish or the mount that held the petri dish). Each salticid was tested repeatedly (up to 5 times per day with 15–30 min between successive tests, then on successive days for up to 3 days) until it either displayed or reached the top of the ramp. No individual was used again after it provided data once for discrimination distance.

Thirty-seven species were tested. Three were lyssomanines, 8 were spartaeines and 26 were salticines (Table 1). The species were from North and Central America, Europe, Africa, the Middle East, Asia, Australia and New Zealand. Natural habitats ranged from rain forest to desert. From previous studies we know the displays typically adopted in interactions with conspecifics (references in Table 1).

Table 1. Species of salticid used in the study. All information is for adult males

Species	Sub-family[a]	N[b]	Body length (mm)[c]	Collection site(s) (display and body length)	Reference
Asemonea tenuipes O.P.-Cambridge	Lys	12	5	Sri Lanka	Jackson & Macnab (1991)
Goleba puella (Simon)	Lys	16	5	Kenya	Jackson & Macnab (1991)
Lyssomanes viridis (Walckenaer)	Lys	20	6	U.S.A. (South East)	Jackson & Macnab (1991)
Brettus adonis Simon	Spa	16	4	Sri Lanka	Jackson & Hallas (1986*b*)
Brettus cingulatus Thorell	Spa	15	4	Sri Lanka	Jackson & Hallas (1986*b*)
Cyrba algerina (Lucas)	Spa	22	4	France, Portugal & Spain	Jackson & Hallas (1986*b*)
Cyrba ocellata (Kroneberg)	Spa	18	5	Sri Lanka	Jackson (1990)
Portia africana (Simon)	Spa	18	6	Kenya	Jackson & Hallas (1986*a*)
Portia fimbriata (Doleschall)	Spa	37	6	Australia (Queensland)	Jackson & Hallas (1986*a*)
Portia labiata (Thorell)	Spa	19	6	Sri Lanka	Jackson & Hallas (1986*a*)
Portia schultzi Karsch	Spa	21	6	Kenya	Jackson & Hallas (1986*a*)
Bavia aericeps Simon	Sal	23	13	Australia (Queensland)	Jackson (1986*a*)
Cobanus mandibularis Peckham & Peckham	Sal	20	6	Costa Rica	Jackson (1989)
Corythalia canosa (Walckenaer)	Sal	24	5	U.S.A. (Florida)	Jackson & Macnab (1989*a*)
Cosmophasis micarioides (L. Koch)	Sal	23	7	Australia (Queensland)	Jackson (1986*b*)
Epeus sp.	Sal	18	8	Singapore	Jackson (1988*a*)
Euophrys parvula Bryant	Sal	20	6	New Zealand (South Island)	Wells (1988), Jackson & Willey (1995)
Euryattus sp.	Sal	22	8	Australia (Queensland)	Jackson (1985*a*)
Helpis minitabundus (L. Koch)	Sal	19	8	New Zealand (North Island)	Jackson, unpublished
Holoplatys sp. indet.	Sal	18	4	New Zealand (South Island)	Jackson & Harding (1982)
Jacksonoides queenslandica Wanless	Sal	22	6	Australia (Queensland)	Jackson (1988*b*)
Marpissa marina Goyen	Sal	17	6	New Zealand (South Island)	Jackson, Polard *et al.* (1990)
Menemerus sp.	Sal	15	4	Kenya	Jackson (1986*c*)
Mogrus neglectus (Simon)	Sal	22	8	Israel	Jackson, unpublished
Mopsus mormon Karsch	Sal	20	12	Australia (Queensland)	Jackson (1983)
Myrmaraclme lupata L. Koch	Sal	19	8	Australia (Queensland)	Jackson (1982*a*)
Myrmarachne plataleoides O.P.-Cambridge	Sal	18	9	Sri Lanka	Nelson & Jackson, unpublished
Natta rufopicta Simon	Sal	18	5	Kenya	Jackson (1986*d*)
Phidippus femoratus (Peckham & Peckham)	Sal	20	8	U.S.A. (Arizona)	Jackson (1982*b*)
Phidippus johnsoni (Peckham & Peckham)	Sal	20	9	U.S.A. (California)	Jackson (1978)
Phintella sp.	Sal	14	6	Philippines (Luzon)	Nelson & Jackson, unpublished
Plexippus paykulli (Savigny & Audouin)	Sal	19	9	U.S.A. (South East)	Jackson & Macnab (1989*b*)
Simaetha paetula (Keyserling)	Sal	20	7	Australia (Queensland)	Jackson (1985*b*)
Tauala lepidus Wanless	Sal	21	6	Australia (Queensland)	Jackson (1988*c*)
Thorelliola ensifera (Thorell)	Sal	17	5	Singapore	Jackson & Whitehouse (1989)
Trite auricoma Urquhart	Sal	22	8	New Zealand (South Island)	Jackson, unpublished
Trite planiceps Urquhart	Sal	25	10	New Zealand (South Island)	Taylor & Jackson, unpublished

[a] Lys = Lyssomaninae; Spa = Spartaeinae; Sal = Salticinae.
[b] Number of tests in which a display occurred (non-display tests are not included, see text).
[c] Mean body length, anterior margin of cephalothorax to posterior tip of abdomen, from previous studies. See reference column.

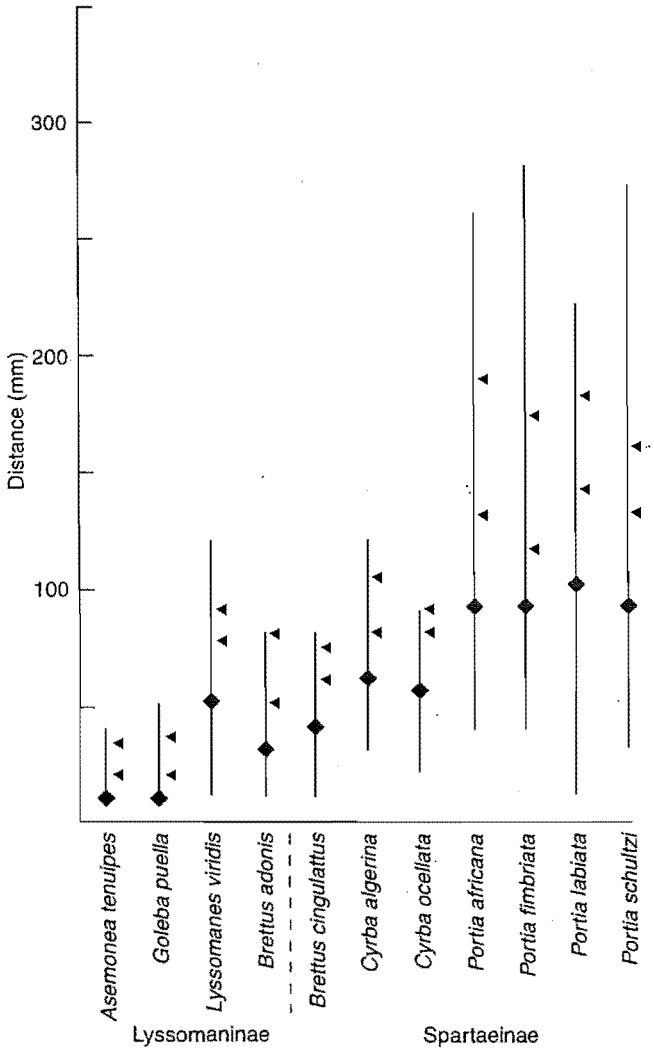

Fig. 2. Distances at which spartaeine and lyssomanine salticids displayed at mirror image. Bar: spread of data (between maximum and minimum); diamond: median; arrows: point above which 25% and 90% of sample lies on bar.

RESULTS

All species displayed to mirrors, and none displayed to insects. For each species, display distances tended to vary considerably among individuals (Figs 2 & 3) and were not normally distributed. The medians for most species were between 50 and 100 mm (10 and 20 body lengths). Maximum display distances for most tended to be about twice as large as the median, and always greater than 10 body lengths. Two lyssomanines, *Asemonea tenuipes* and *Goleba puella*, were exceptions, each having median and maximum display distances of < 10 body lengths.

With the exception of two genera, the lyssomanines and spartaeines tended to have shorter mean and maximum display distances than the salticines. *Lyssomanes viridis* was an exception among the lyssomanines, having display distances that overlapped the lower end of the distribution for salticines. Among the spartaeines, *Portia* was an exception, the five species tested having display distances comparable to the top end of the salticines' distribution. Display distances of all other spartaeines studied resembled those of *L. viridis* by overlapping the lower end of the salticine range. Among the salticines, the two ant-mimicking species tested (both in the genus *Myrmarachne*) had especially short display distances.

DISCUSSION

Salticid males generally do not tolerate each other in close proximity, but instead interact using species-specific threat displays, sometimes escalating to physical combat before one individual flees from the other (Jackson, 1982*c*; Jackson & Pollard, 1997). Different displays are used by a male when interacting with a female (courtship), and an insect generally elicits no display at all, as our results show.

In the present study, displays provided evidence that males identified their own mirror images as rival conspecific males. Males of all species used their typical male–male threat displays when tested with mirrors, but never displayed when tested with insects. That identification was by optical cues alone is implied because using a mirror ruled out cues from chemicals, sound or substrate-borne vibration.

Display by a salticid at a given distance from the mirror indicates an ability to identify rivals from distances at least that far away, but failure to display does not indicate an inability to make an identification. Other factors, such as attention and motivation, may influence display distance (Crane, 1949). Despite being close enough to identify a rival, a salticid might fail to do so because its attention is on other objects in the environment. Even when a salticid identifies a rival that is far away, it may become motivated to display only when closer.

In our study, inter-individual variation in attention and motivation may account for the wide intraspecific spread in the distribution of display distances. The possibility that interspecific variation in display distances is primarily a consequence of variation in attention and motivation cannot be ruled out. However, the most reliable indication of ability, instead of attention and motivation, should be the upper ends of the distributions of display distances. Maximum discrimination distances, the top 10% of a sample, or the top 25% of a sample serve better than the medians and means as indicators of visual discrimination ability (Figs 2 & 3).

From the upper end of the distributions it can be concluded that distances at which most salticids make meaningful discriminations are more like those found by Jackson & Blest (1982) than those suggested by Drees (1952). When maximum display distances are plotted against each species' body length (Fig. 4), it appears that larger spiders usually display at mirrors from farther away. Such a relationship is not unexpected

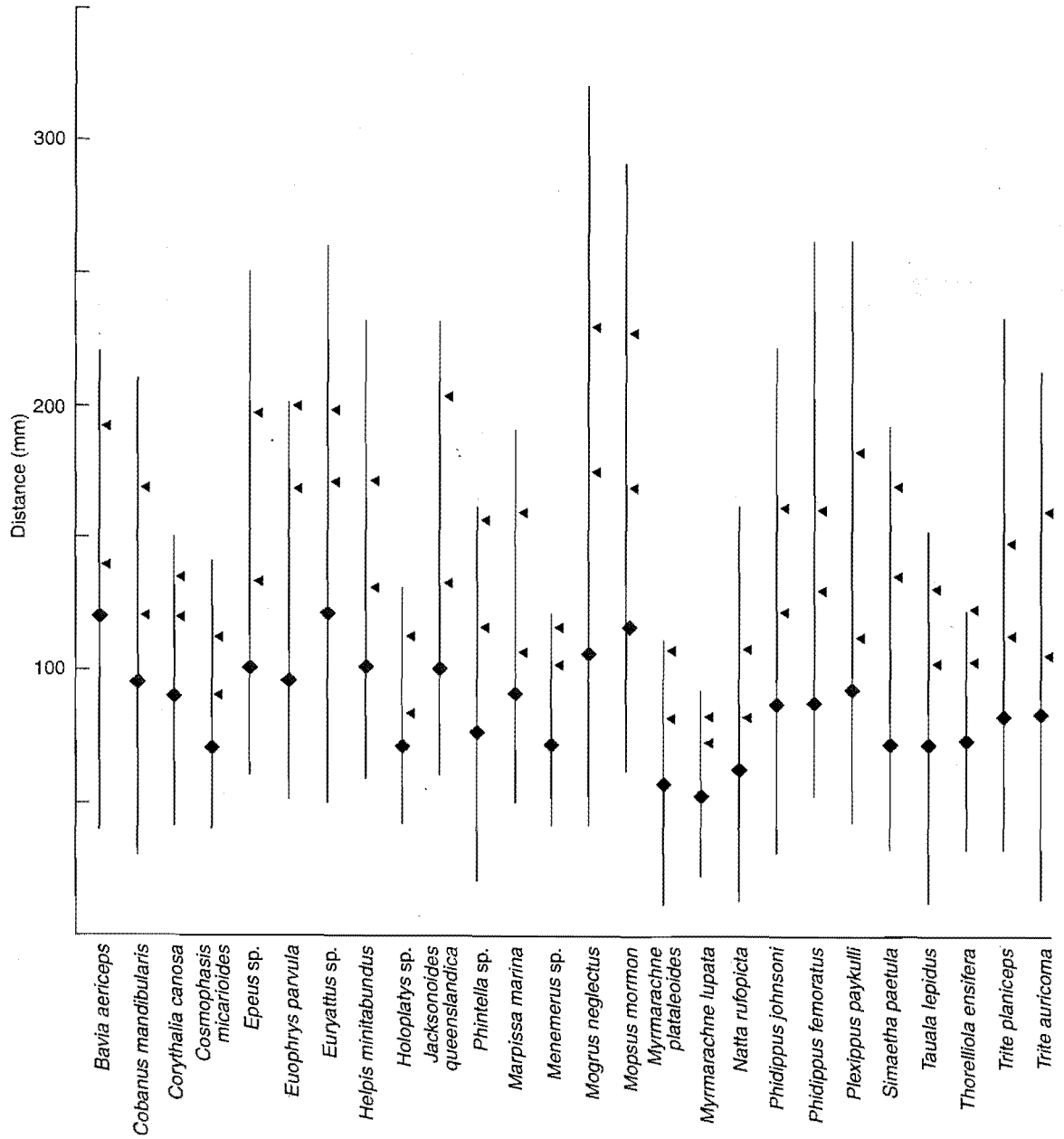

Fig. 3. Distances at which salticine salticids displayed at mirror image. Bar: spread of data (between maximum and minimum); diamond: median; arrows: point above which 25% and 90% of sample lies on bar.

because increased body size will generally reduce the difficulty of the identification task and increase the distance at which the task can be carried out by providing physically larger and thereby more noticeable identification cues from a conspecific. In addition, larger eyes can potentially provide better spatial acuity and light gathering ability than smaller eyes (Land, 1981). However, a detailed discussion of the effects of body and eye size on spatial acuity is beyond the scope of this study.

Discrimination distance maxima appear to relate to the organization of the AM foveal layer I sampling mosaics. Lyssomanine and spartaeine salticids probably branched off early from the lineage that gave rise to the salticines (Rodrigo & Jackson, 1992). Among the lyssomanines, *Goleba puella* probably branched off earlier than the other species within this subfamily (Wanless, 1980) and has the most poorly ordered layer I rhabdomeral sampling mosaic known for any salticid studied (Blest, O'Carroll & Carter, 1990), i.e. a network in which each receptor cell has two rhabdomeres and rhabdomeres in neighbouring receptors touch. Discrimination-distance scores were especially low for *G. puella* (max. 50 mm or 10 body lengths). Discrimination-distance scores for another lyssomanine, *Asemonea tenuipes* (max. 40 mm or 8 body lengths) were comparable to those for *G. puella*. The retinal organization of *A. tenuipes* has not been investigated, but our data suggest that *A. tenuipes* may resemble *G. puella* by having an optically inferior sampling mosaic.

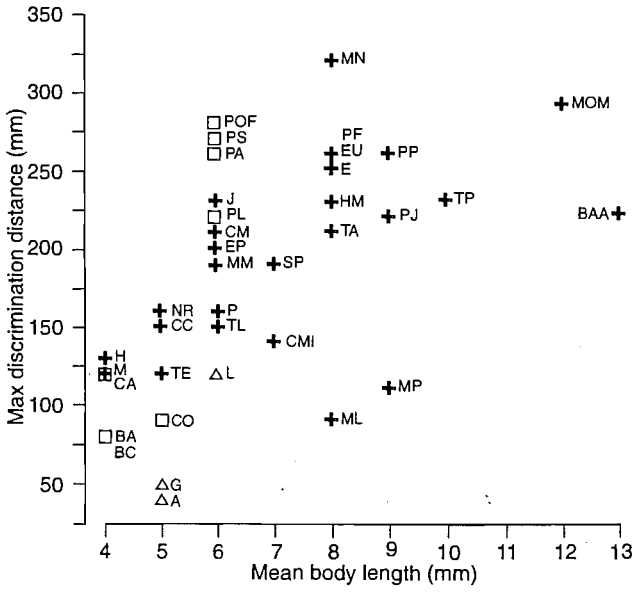

Fig. 4. Maximum display distance plotted against mean body length (Table 1). Lyssomaninae, triangles: *Asemonea tenuipes*, A; *Goleba puella*, G; *Lyssomanes viridis*, L. Spartaeinae, squares: *Brettus adonis*, BA; *Brettus cingulattus*, BC; *Cyrba algerina*, CA; *Cyrba ocellata*, CO; *Portia africana*, PA; *Portia fimbriata*, POF; *Portia labiata*, PL; *Portia schultzi*, PS. Salticinae, crosses: *Bavia aericeps*, BAA; *Cobanus mandibularis*, CM; *Corythalia canosa*, CC; *Cosmophasis micarioides*, CMI; *Epeus* sp., E; *Euophrys parvula*, EP; *Euryattus* sp., EU; *Helpis minitabundus*, HM; *Holoplatys* sp., H; *Jacksonoides queenslandica*, J; *Marpissa marina*, MM; *Menemerus* sp., M; *Mogrus neglectus*, MN; *Mopsus mormon*, MOM; *Myrmarachne lupata*, ML; *Myrmarachne plataleoides*, MP; *Natta rufopicta*, NR; *Phidippus femoratus*, PF; *Phidippus johnsoni*, PJ; *Phintella* sp., P; *Plexippus paykulli*, PP; *Simaetha paetula*, SP; *Tauala lepidus*, TL; *Thorelliola ensifera*, TE; *Trite auricoma*, TA; *Trite planiceps*, TP.

It seems that retinal organization has influenced discrimination-distance scores of *Cyrba algerina* (max. 120 mm or 30 body lengths), a spartaeine. The retinae of *C. algerina*, although more organized than those of *G. puella*, have two rhabdomeres per receptor cell throughout the fovea of layer I, but at the outer margin of the fovea, the first three rows of rhabdomeres are very short and each receptor has only a single isolated rhabdomere at its anterior end (Blest, O'Carroll *et al.*, 1990). Discrimination scores of *C. algerina* and a congeneric species, *C. ocellata*, in the present study were intermediate between the scores of *G. puella* and those of most salticines.

Discrimination-distance scores for *Lyssomanes viridis* (max. 120 mm or 24 body lengths) were the largest for the three lyssomanines. This is consistent with *L. viridis* having a sampling mosaic that, although less organized than that of salticines, appears to be considerably better than that of *G. puella*. It is interesting that the sampling mosaic of *L. viridis*, which has only one rhabdomere per receptor in foveal layer I (Blest & Sigmund, 1984), is perhaps superior to that of *C. algerina* which is intermediate between the crude rhabdomeral network of *Goleba* and the well-ordered state of *Portia* and the Salticinae. Yet the present study provides no evidence that *L. viridis* and *C. algerina* have different discrimination distances.

Of the salticines investigated here, only the retinae of *Phidippus johnsoni* have been extensively studied (Blest, McIntyre *et al.*, 1988). Consistent with its maximum of 220 mm and 25 body lengths, *P. johnsoni* has a highly organized layer I sampling mosaic. The highest discrimination scores obtained from the Salticinae were for *Mogrus neglectus* (max. 320 mm or 42 body lengths). However, the species with the highest discrimination distance scores in terms of body lengths was a spartaeine (Fig. 4), *Portia fimbriata*. Maximum discrimination distance for *P. fimbriata* was 47 body lengths (280 mm).

The four *Portia* species studied had discrimination-distance scores comparable with, if not greater than, most of the salticines studied. However, information on retinal structure is available only for *P. fimbriata*, which has a retinal organization that is in most respects comparable to that of an advanced salticine eye (Blest, 1988; Blest, O'Carroll *et al.*, 1990).

Two salticine species, *Myrmarachne plataleoides* and *M. lupata*, had especially low discrimination distances (Figs 3 & 4). *Myrmarachne* is a genus of ant-mimicking salticids. *Myrmarachne*'s morphological transformation related to ant mimicry may have implications for its relatively poor discrimination distances. Further study of the eyes and discrimination processes used by *Myrmarachne* would be useful for clarifying potential trade-offs between high acuity vision and ant mimicry.

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Chapter 5. Prey classification by *Portia fimbriata*

This chapter has been submitted to the *Journal of Zoology* (*London*). The text is presented here in the same format as the submitted manuscript. Figures and their captions have been placed close to where they are referenced in the text and tables follow the text.

PREY CLASSIFICATION BY PORTIA FIMBRIATA,

A SALTICID SPIDER THAT SPECIALIZES AT PREYING

ON OTHER SALTICIDS:

SPECIES THAT ELICIT CRYPTIC STALKING

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Key words: Portia fimbriata, Salticidae, spiders, predation, vision

ABSTRACT

Portia fimbriata from Queensland, Australia, is an araneophagic jumping spider (Salticidae) that includes in its predatory strategy a tactic (cryptic stalking) enabling it to prey effectively on common sympatric salticids from other genera. Using standardised tests in which only optical cues were available (prey enclosed in small glass vial within large cage), P. fimbriata's reactions to 114 salticid species were investigated. Except for Myrmarachne spp. (ant mimics), all salticids tested triggered cryptic stalking by P. fimbriata. This included not only sympatric, but also allopatric, salticids. The salticid on which P. fimbriata most commonly preys in nature is Jacksonoides queenslandicus, but cryptic stalking was triggered by species with considerably different appearance, including beetle mimics, species with unusual body shapes, and species with a wide variety of camouflaging markings. P. fimbriata was also tested with lycosid, clubionid, theridiid and desid spiders and with flies and ants, but none of these arthropods triggered cryptic stalking. Optical cues used by P. fimbriata for discrimination between salticid and non-salticid prey are discussed.

INTRODUCTION

Jumping spiders (Salticidae) are distinctive because of acute vision and complex predatory behaviour (Forster, 1982; Land, 1985; Jackson & Pollard, 1996; Harland, Jackson & Macnab, 1999). Eight eyes are spaced around their cephalothorax, the six more laterally positioned eyes being called the 'secondary eyes' and the two very large forward-facing antero-median eyes being known as the 'principal eyes'. Secondary eyes function primarily as movement detectors (Land, 1971; Duelli, 1978), but the salticid's principal eyes, which are considerably larger than the antero-median eyes of spiders from any other family, are responsible for acute vision (Land, 1969; Blest, McIntyre, & Carter, 1988; Blest, O'Carrol, & Carter, 1990).

Most salticids are strictly hunting spiders, and primarily insectivorous (Richman & Jackson, 1992; Jackson & Pollard, 1996). Portia is exceptional because the species in this salticid genus are versatile predators which prefer other spiders as prey (Li, Jackson, & Barrion, 1997). Besides stalking prey away from webs, these remarkable salticids build their own prey-capture webs and also make predatory raids into other spiders' webs where they take insects, the resident spider and its eggs. Spiders in alien webs are not simply stalked or chased down, but instead deceived and manipulated by aggressive-mimicry signals (Wilcox & Jackson, 1998).

Among species and populations of Portia studied, the Queensland P. fimbriata is exceptional because its preferred prey are from other genera of salticids (Li & Jackson, 1996). Nesting salticids are enticed out of their nests by aggressive-mimicry signals and a special tactic, cryptic stalking, enables the Queensland P. fimbriata to be exceedingly effective at capturing salticids in the open, away from nests and webs (Jackson & Blest, 1982).

Portia does not look like a typical salticid - nor even like an animal. In a web, it resembles a piece of detritus (Wanless, 1978a), and when walking, its slow, choppy gait is

unlike that of any other salticid. When resting in a web, Portia adopts a special posture, called the 'cryptic rest posture', by pulling legs in close to the body and palps back beside the chelicerae (Jackson & Blest, 1982). When cryptic stalking, the Queensland P. fimbriata holds its palps back beside its chelicerae, as in the cryptic rest posture, and exaggerates the slow, choppy gait of its normal locomotion. If faced by its salticid prey, P. fimbriata freezes until the prey faces away again. When stalking any other type of prey, P. fimbriata does not pull its palps back and does not routinely freeze if faced. Most salticids fail to recognize a cryptically stalking P. fimbriata as a predator, but they often defend themselves when stalked by other species of Portia (Jackson & Hallas, 1986).

Cursorial salticids are especially abundant in the habitat of the Queensland Portia, and cryptic stalking appears to be a local adaptation to these locally abundant prey (Jackson & Blest, 1982). Although many species of salticids are found in the Queensland rain forest, one species, Jacksonoides queenslandicus, appears to be by far the most abundant on the tree trunks, boulders and rock walls in the microhabitat of P. fimbriata (Jackson, 1988). The disproportionate abundance of J. queenslandicus within P. fimbriata's environment suggests that J. queenslandicus, rather than salticids in general, might have been responsible for the evolution of cryptic stalking.

Regardless of whether cryptic stalking evolved primarily as a tactic for use against J. queenslandicus, the cues that elicit cryptic stalking might be general to many or most salticid species or specific to J. queenslandicus. In the present study, we investigate how readily P. fimbriata adopts cryptic stalking against a wide range of different species of prey, effectively asking P. fimbriata to tell us what species it classifies as salticids.

MATERIALS AND METHODS

Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier spider studies (Jackson and Hallas, 1986). Testing was carried out between 0900 h and 1700 h (laboratory photoperiod 12L:12D, lights at 0800). No individual Portia was used in more than one test.

In each test there was one 'test spider', P. fimbriata, and one prey animal, a spider or an insect (Table 1-6). Prey were either collected from the field or derived from laboratory culture. All test spiders were from laboratory culture. Except for conspecifics in eggsacs before dispersal, test spiders had prior contact with no salticids of any species, nor with clubionids, lycosids or ants.

Each P. fimbriata was either a juvenile (4-8 mm in body length) or an adult female (8-10 mm body length). No subadult (one instar previous to maturity) or adult males were tested. Hunger state was standardized before testing by keeping each P. fimbriata without prey for 3-5 days.

Tests were staged in a rectangular chamber (internal dimensions: 30 mm wide, 95 mm long, 83 mm high). The two narrow walls, the floor and the roof were wood, whereas the wide sides were made of transparent glass (Fig. 1). The glass walls could be slid out to facilitate cleaning of the chamber. Two holes (diameter 15 mm), one on each of the wooden walls (centred 30 mm below the top of the frame), allowed introduction of Portia and presentation of prey. A transparent glass vial (diameter 15 mm) was positioned inside the prey-presentation hole so that the open end was flush with the outside of the cage and the rest protruded 35 mm into the chamber. During tests, a prey animal was inside the tube and the open end was stoppered.

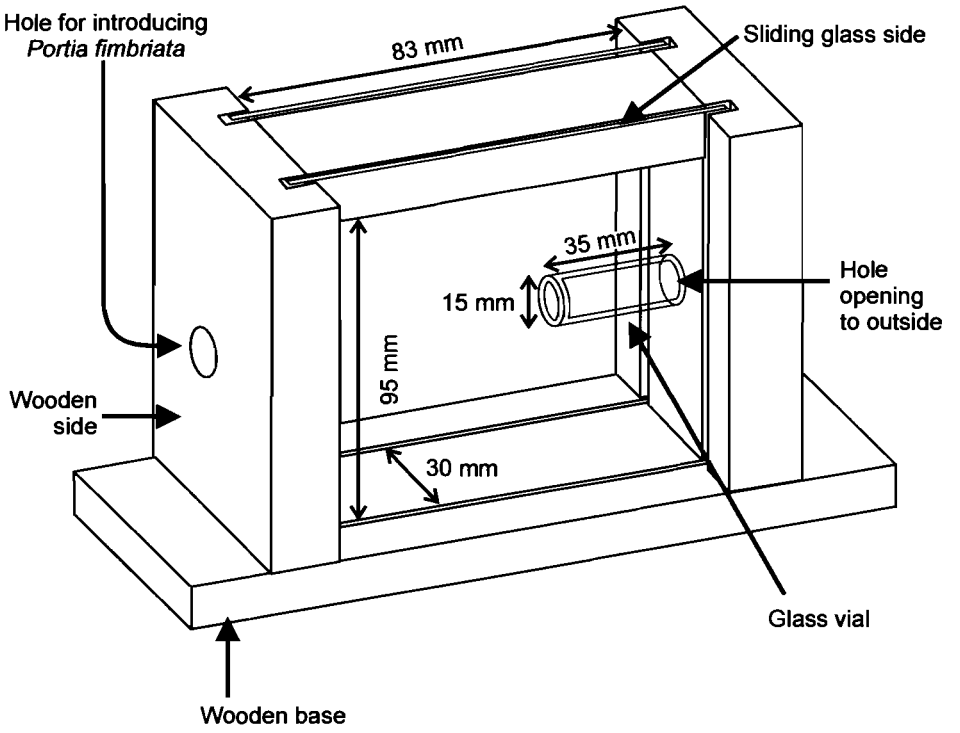

Fig. 1. Apparatus used in formal tests (wooden frame with two sliding glass sides). To start test, glass vial, with prey animal sealed inside, inserted into chamber. Portia fimbriata introduced through hole (stoppered during test) in opposite end. Glass walls slide out to allow cleaning of apparatus between tests.

Before starting a test, a P. fimbriata was transferred from a 30-mm long plastic tube (diameter 15 mm; stoppered at one end) into the chamber by placing the open end of the tube flush with the open introduction hole, then removing the stopper from the tube and prodding the spider with a small brush until it passed through the introduction hole. The introduction hole was then stoppered and remained stoppered during tests.

Test spiders could see prey inside the vial, but potential chemical cues from prey were ruled out because the vial was kept stoppered. Between tests, the glass sides were removed and the entire chamber was washed with water and 80% ethanol, then allowed to dry before subsequent testing. Washing ruled out the potential of chemical influences from previous test spiders.

Stalking was defined as steady head-on movement toward prey in vials. Test results were recorded as 'did not stalk' when P. fimbriata failed to begin stalking prey within 60 min after a test began. When a test spider began stalking, its behaviour was recorded until it walked onto the vial, it stood stationary facing the vial from less than 5 mm away for 5 min or 60 min elapsed, whichever happened first.

Three categories of stalking behaviour were recognized: cryptic stalking, defined by consistent adoption of the retracted-palps posture and freezing when faced by a prey no more than 50 mm away; ordinary stalking, consistent adoption of the same posture as used during ordinary locomotion, including holding the palps loosely in front of the chelicerae, but failure to freeze when faced by prey no more than 50 mm away; ambivalent stalking, sometimes adopting the retracted-palps posture or sometimes freezing when faced by prey that is no more than 50 mm away, but failing to do so consistently.

We used 145 species of salticids as prey. However, based on appearance, we distinguished 200 "categories" (Table 1-5). Some species provided two categories for testing

purposes because, although large juvenile and adult female salticids tend to be similar in appearance, adult males are often considerably divergent. Eighteen salticid species (25 categories) were sympatric with Queensland P. fimbriata. Unless otherwise stated, we use the terms 'male' and 'female' to refer to adult male and adult female, respectively, and 'juvenile' to refer to immature salticids regardless of sex.

Baseline data were collected by testing P. fimbriata with representative insect and non-salticid spider species on which it is known to prey (clubionid, lycosid, theridiid, fruit fly, house fly) and six beetle species (Table 6). There were two categories of lycosids, eggless and egg-carrying females.

A sizeable minority of salticids is ant-like in appearance, the largest and most extensively studied being in the genus Myrmarachne (Wanless, 1978b). Resemblance to ants probably functions primarily as Batesian mimicry (Edmunds, 1974; Jackson, 1986; Jackson & Willey, 1994): deterrence with optical cues of predators that are adverse to attacking ants. As P. fimbriata has never been observed feeding on ants, we were especially interested in P. fimbriata's reaction to ant-like salticids. We tested 23 species from the genus Myrmarachne (Fig. 2a) plus representatives of another two genera of ant-like salticids, Peckhamia and Synageles (Table 5). Tests using four species of real ants (Fig. 2b; Table 6) provided a baseline against which to compare findings from tests where we used ant-like salticids.

Besides tests with prey in vials, qualitative information came from informal testing of P. fimbriata with each prey category in the absence of vials where prey capture could take place. The test spider and prey were placed together on a leaf or a piece of bark, or in a clean cage, and watched for 60 min or until predation took place. P. fimbriata was tested with each type of prey repeatedly (on different days) until predation was observed or until 10 tests had been completed. In these tests no ants and no Myrmarachne spp. were stalked or attacked, but

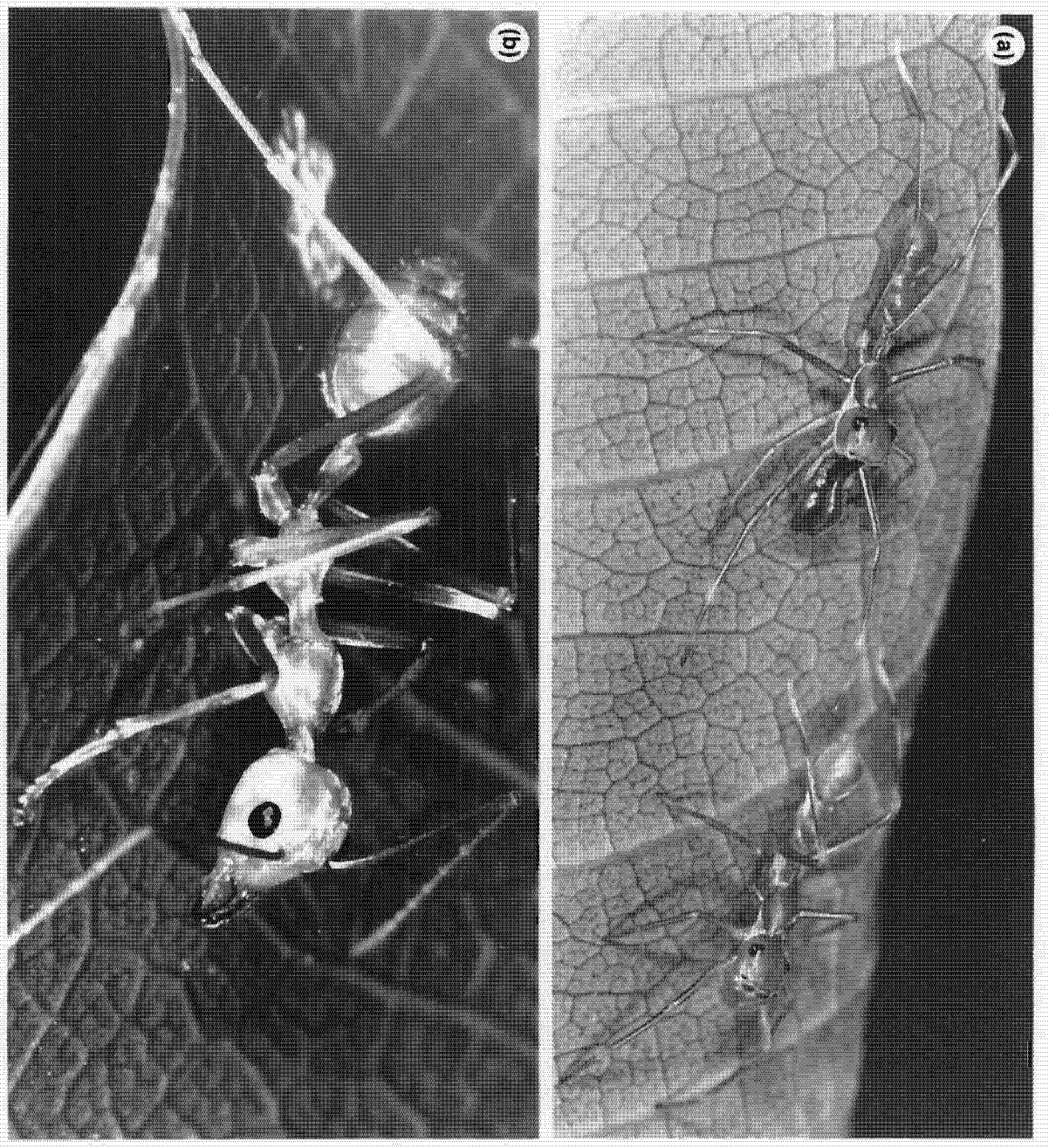

Fig. 2. Salticid ant mimics and an ant. a. Myrmarachne assimilis (left) mature male and (right) mature female. b. Worker of Oecophylla smaragdina.

at least one individual of each other species and category of prey was captured and fed on. Findings given below all come from formal testing with prey in vials.

RESULTS

P. fimbriata never stalked the ants (Fig. 2b; Table 7), Myrmarachne spp. (ant-mimics) (Fig. 2a; Table 6), or beetles (Table 6). Only 35% and 25% stalked Musca domestica (house fly) and Drosophila melanogaster (fruit fly), respectively, and there were no instances of cryptic or ambivalent stalking against any of these prey. Other than salticids, the most frequently stalked prey were two web-building spiders, Achaearanea sp. (90%) and Badumna longinquus (75%) (Table 6), but only ordinary stalking was used with these. P. fimbriata never adopted full cryptic stalking with wolf spiders regardless of whether they were carrying eggs or not, but ambiguous stalking was adopted twice against an eggless and once against an egg-carrying lycosid. Clubionids were never stalked at all.

Cryptic stalking was adopted by P. fimbriata against all salticid categories other than Myrmarachne spp. To assist with presentation, we assigned the salticid categories that were stalked (i.e., those other than Myrmarachne spp.) to five groups, using the ratios of P. fimbriata that adopted the three different stalking styles (cryptic, ordinary and ambivalent) to define each group.

Salticids against which P. fimbriata always stalked and against which the style was always cryptic stalking were put in Group A (Table 1). Group A was the largest (60 categories). Salticids against which P. fimbriata usually (in at least 70% of the tests), but not always, stalked, with cryptic stalking always being they style adopted, went into Group B (Table 2). There were 48 categories (all of which were salticids) in Group B. Categories against which P. fimbriata adopted cryptic stalking, but also occasionally (in no more than

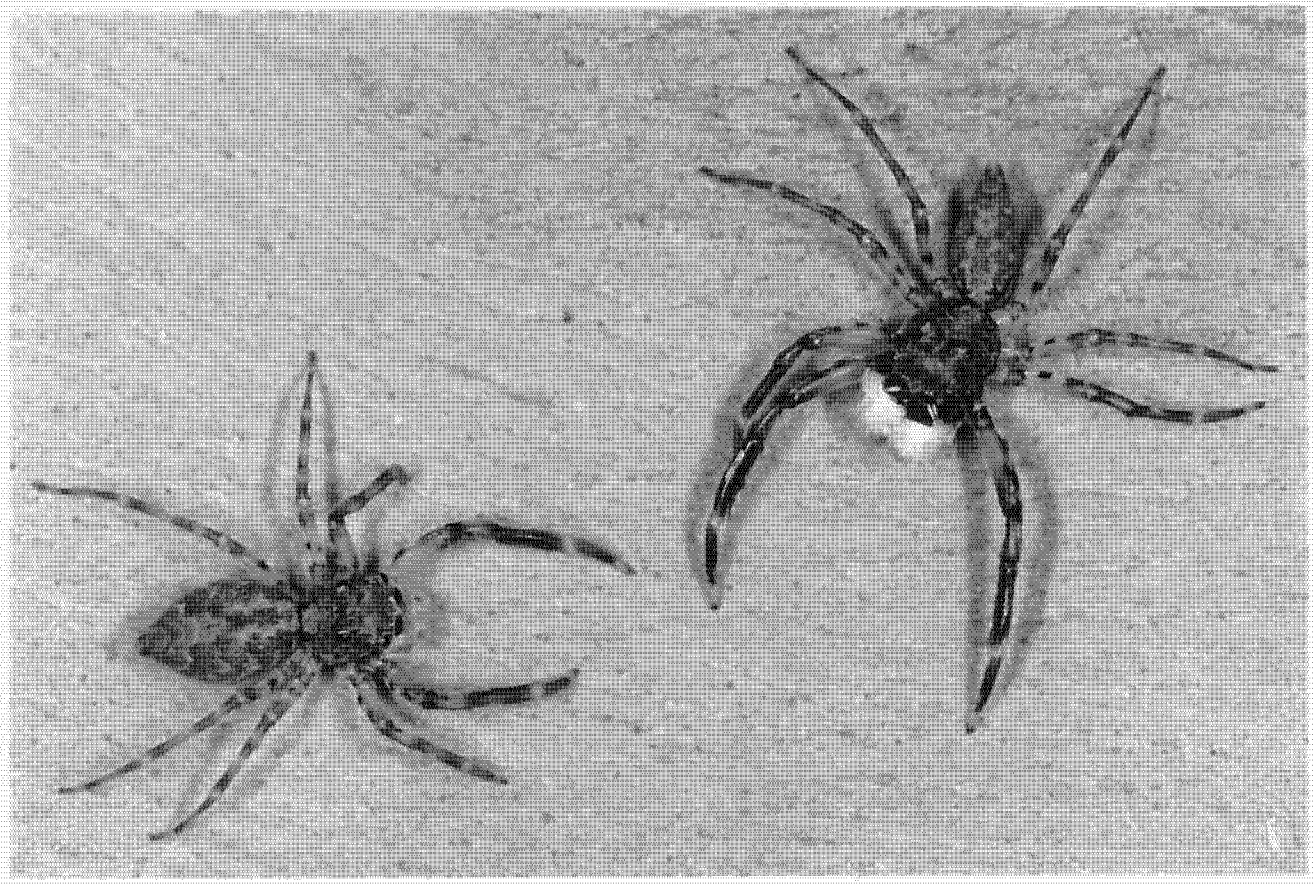

Fig. 3. Jacksonoides queenslandicus, common salticid prey of P. fimbriata, top profiles of (left) mature female and (right) mature male.

15% of the tests) adopted ambivalent stalking, formed Group C (Table 3). There were 38 categories (all of which were salticids) in Group C. P. fimbriata never adopted ordinary stalking against categories in Group A, B or C.

J. queenslandicus males (Fig. 3a) and females (Fig. 3b) fell into Group A and C, respectively. Although, Groups A, B and C, included salticids that more or less resemble J. queenslandicus, these groups also included salticids that, to the human eye, were considerably different. Holoplatys sp. (Fig. 4a), being dorso-ventrally flattened to an unusual extent, and Mantisatta longicauda (Fig 4b), having an unusually elongated and narrow body, are especially striking examples.

There were 15 categories of salticids against which P. fimbriata adopted cryptic stalking and also, occasionally adopted ordinary stalking (never in more than 15% of tests). These were assigned to Group D (Table 4). Females of Cyrba algerina, the only salticid tested from the same subfamily (Spartaeinae) as Portia, fell into Group D. To the human eye, this species may not appear so different from J. queenslandicus in appearance. However, some other members of Group D were clearly more atypical in appearance. For example, Holoplatys planissimus, like its congener in Group C, is dorso-ventrally flattened. Thiania bhamoensis is highly iridescent. Heretemita alboplagiata (Fig. 5a), Simaethula sp. (Fig. 5b) and especially Sassacus papenhoei (Fig. 5c) resemble beetles: cephalothorax and abdomen appear to fit together seamlessly, mimicking somewhat the appearance of a beetle's thorax adjoining its elytra-covered abdomen. Marengo spp. bear a passing resemblance to psuedoscorpions (Wanless, 1978c). When viewed head on, Mopsus mormon males have a striking appearance (Fig. 6): black carapace bordered by white fringes of hair that rise up the margins of the face to a peak surmounted by a topknot of black hairs. Lyssomanine salticids are of special interest because the females and juveniles, but not the males, of these

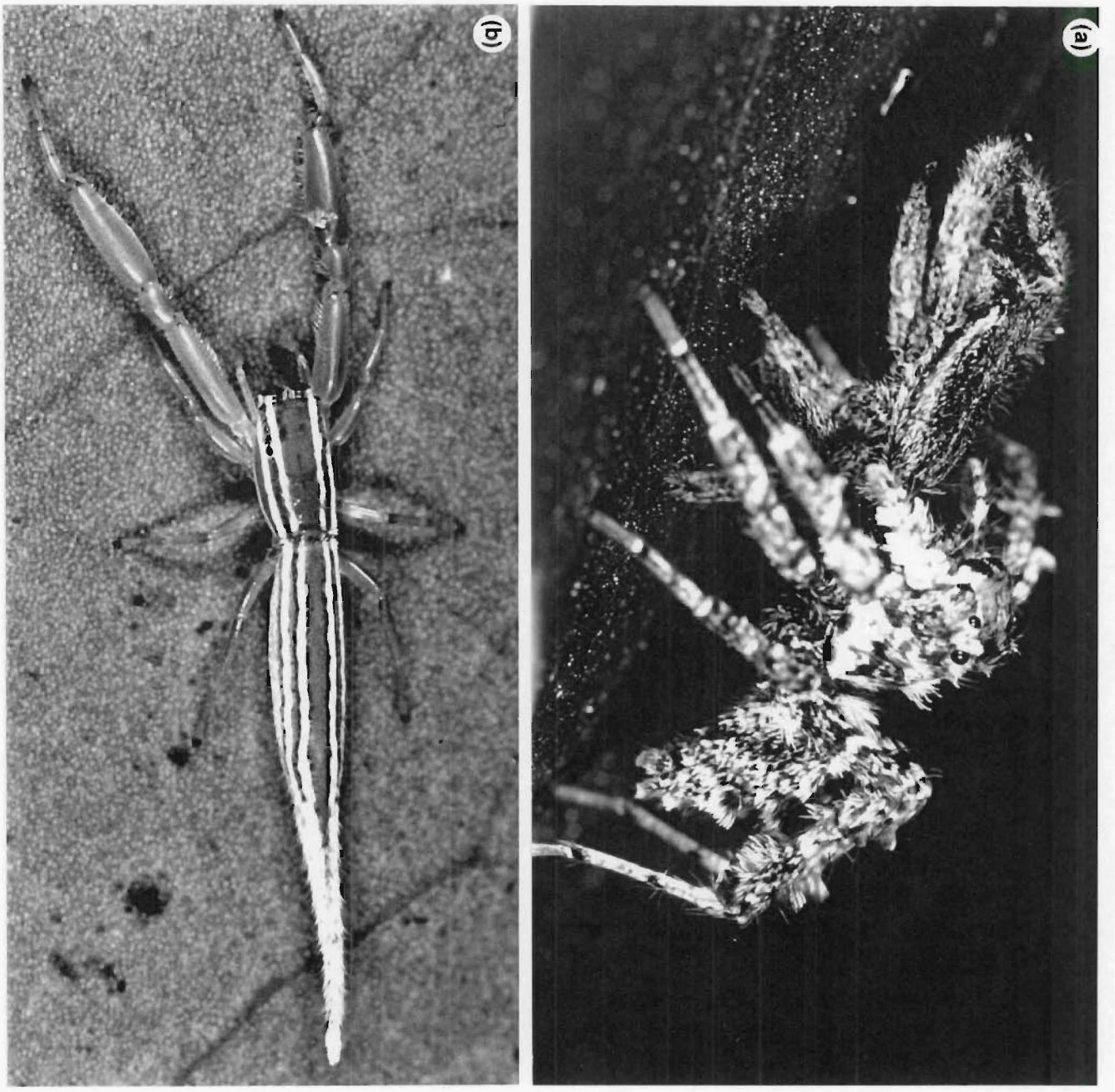

Fig. 4. Salticid prey of P. fimbriata with unusual body shapes. a. Dorsally compressed Holoplatys sp. mature female, after capture by P. fimbriata. b. Dorsal view, longitudinally elongated Mantisatta longicauda mature female.

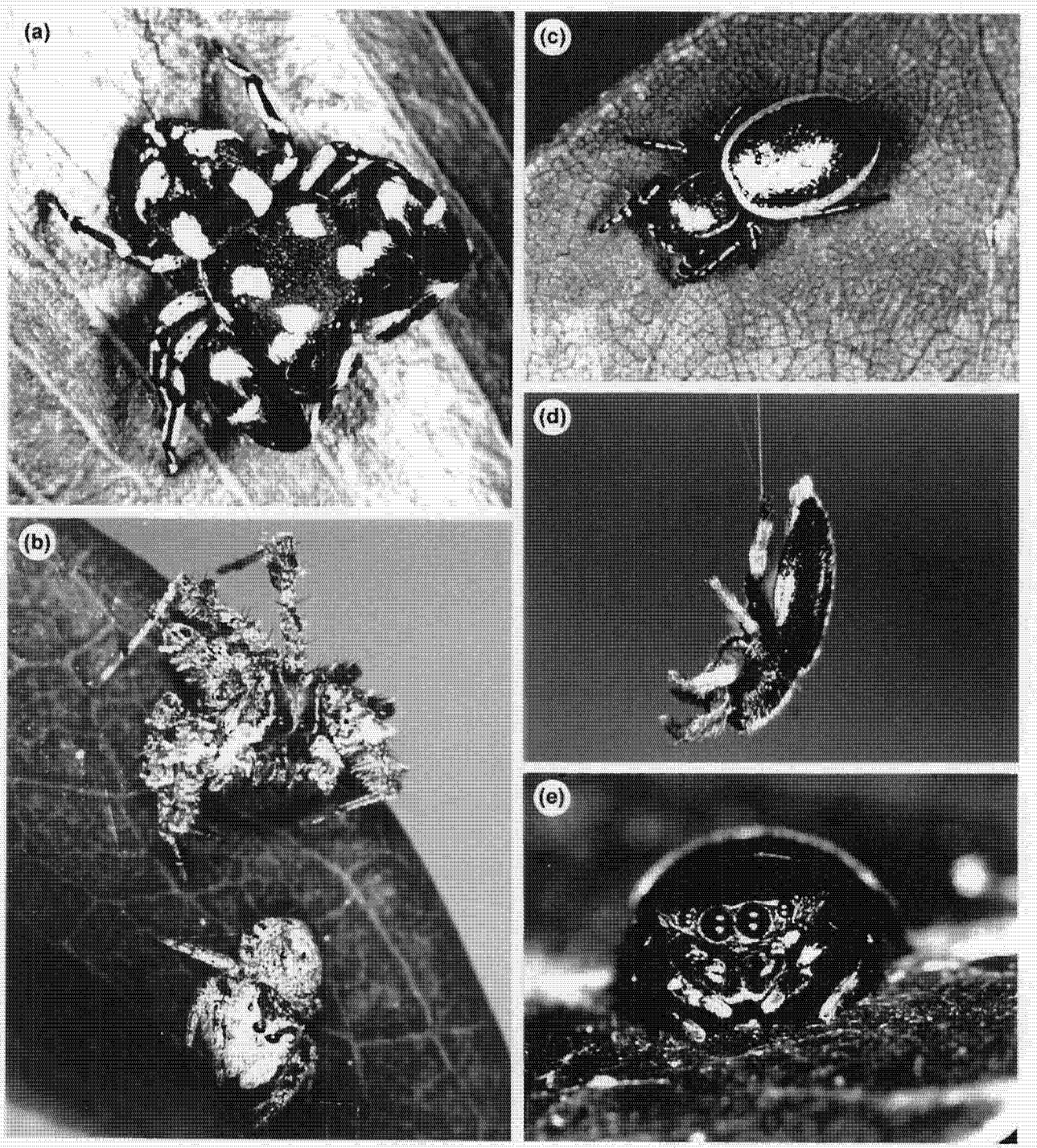

Fig. 5. Salticid beetle mimics. a. Heretemita alboplagiata mature male. b. Simaethula sp. mature female being cryptic stalked by female P. fimbriata. c. Sassacus papenhoei mature female. d. Pachyballus cardiforme mature female, side profile and (e) front profile.

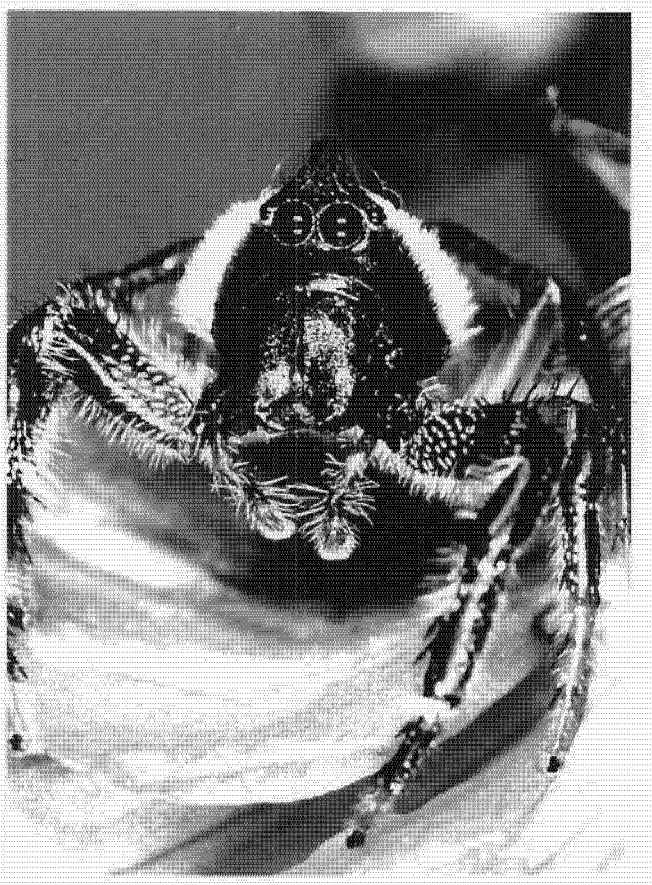

Fig. 6. Mature male Mopsus mormon.

leaf-dwelling species have unusually translucent cuticle. Except for Asemonea murphyae (Group C), all of the lyssomanine females and juveniles we tested (A. tenuipes (Fig. 7a), Goleba puella, Lyssomanes patens, L. viridis and Onomastus nigricauda) ended up in Group D, yet the males of A. tenuipes (Fig. 7b), G. puella and L. viridis all fell into Group C (for O. nigricauda and L. patens, no males were tested).

There were three categories of salticids against which P. fimbriata adopted cryptic stalking, but only infrequently (in no more than 20% of the tests). These were assigned to Group E (Table 4). Two of these, Peckhamia americana (Fig. 2b) and Synageles dalmaticus, were ant-like species. The third, Pachyballus cardiforme (Fig. 5d, e), is a beetle-like species.

We defined 'getting close' as when P. fimbriata came to within 5 mm of the arthropod in the vial. With one exception, all P. fimbriata were cryptic stalking whenever they got close to a salticid belonging to Group A-D, the exception being one test with a Sassacus papenhoei female (Group D) in which P. fimbriata adopted ambivalent stalking. P. fimbriata got close to another 18 S. papenhoei, but while cryptic stalking in each of these instances. Group-E data were different. Against one S. dalmaticus and three P. cardiforme, P. fimbriata was stalking ambivalently. In two instances, P. fimbriata was cryptic stalking when it got close to a P. cardiforme.

Those P. fimbriata that stalked house flies, fruit flies and lycosid, clubionid, theridiid, and desid spiders usually got close, but they were never cryptic stalking. Few P. fimbriata got close to beetles, ants or Myrmarachne spp., and none were stalking when they did get close.

Data for J. queenslandicus (male and female pooled) were compared with pooled data for all the other salticids (N = 3266) excluding Myrmarachne. There was no statistical evidence that P. fimbriata's tendency to stalk at all, to adopt cryptic stalking, or to get close in

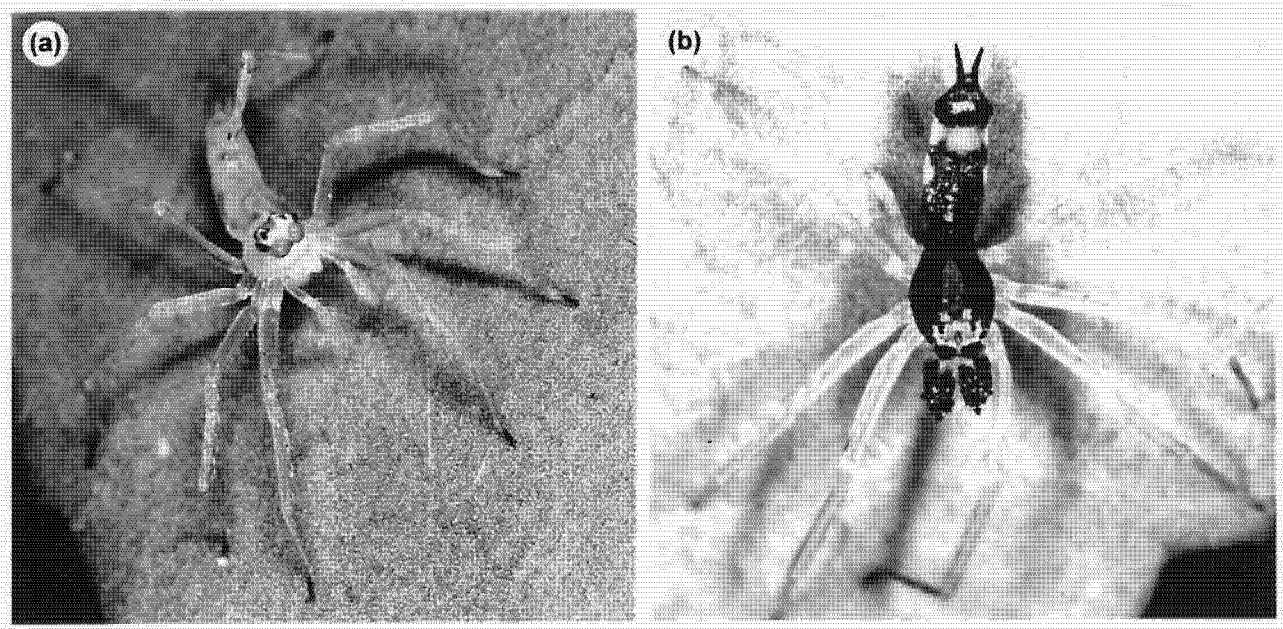

Fig. 7. Asemonea tenuipes (subfamily Lyssomaninae). a. Mature female. b. Mature male.

encounters with J. queenslandicus was greater than in encounters with the other salticids (tests of independence, NS).

DISCUSSION

In our tests, P. fimbriata never adopted cryptic stalking unless the arthropod in the vial was a salticid, confirming that cryptic stalking is a salticid-specific prey-capture behaviour (Jackson & Blest, 1982) and justifying our interpretation of test results as evidence of prey classification. Our tests can be envisaged as letting P. fimbriata tell us, by cryptic stalking or not, when it classified a category of prey as a salticid. Similarly, we discerned when P. fimbriata classified an arthropod as 'non-salticid prey' (approached with ordinary stalking) and 'non-prey' (did not stalked at all), with ambiguous stalking being interpretable as instances where P. fimbriata failed to decide whether the prey was a salticid or not. Our interest is in perception, and no claims about other cognitive processes are intended by the terms 'telling' and 'classifying'.

During both formal and informal testing, cryptic stalking was adopted at least sometimes against each of the 157 salticid categories other than Myrmarachne spp. (i.e., each of these 157 categories was at least sometimes classified by P. fimbriata as a salticid). During both formal and informal testing, P. fimbriata stalked web-building and lycosid spiders, but never used cryptic stalking against these (i.e., P. fimbriata classified these spiders as prey but not as salticids). Although never stalked during formal testing, clubionid spiders appear to be classified as prey because P. fimbriata preyed on them in informal tests, and in these tests only ordinary stalking was observed. Ants and Myrmarachne spp. were never stalked (i.e., P. fimbriata did not classify them as prey) during either formal or informal testing. As ants prey

on P. fimbriata in nature (R. R. Jackson, unpublished), it is likely that aversion, not velleity, accounted for absence of stalking in tests with ants and with Myrmarachne spp.

From experiments in which models (2D drawings and 3D models made of plasticene and wire) were presented to males of Salticus scenicus (Salticidae), Drees (1952) established that leg characteristics (angle to vertical, thickness, and positioning around the body) were critical cues to which this species paid attention. Drees envisaged his experiments as asking S. scenicus to distinguish between only two categories, insects (i.e., prey) and salticids (i.e., conspecifics). When S. scenicus attacked a model, this was taken as evidence that the object had been classified as prey. When S. scenicus displayed, this was taken as evidence that the object had been classified as another salticid. The impression from Drees' study is that S. scenicus uses only leg characteristics (especially thickness, density and a particular angle to vertical, 25°-30°) to identify salticids, with just about any other object of appropriate size being, by default, accepted as prey.

For P. fimbriata, distinguishing insects from salticids is only a small part of what is important. Conspecific salticids are rivals and mates, but other salticids are a type of prey to be pursued by cryptic stalking. 'Prey' for P. fimbriata is not appropriately envisaged as a classification decision arrived at by default. For P. fimbriata, distinguishing salticids from other spiders is instead to distinguish between categories of prey. Some insects are yet another category of prey, whereas ants appear to be identified not as prey but instead as noxious, potentially predatory insects to be avoided. Beetles appear to be neither prey nor enemies.

Although leg characteristics may be the primary cues used by S. scenicus for classifying arthropods as salticids, P. fimbriata adopted cryptic stalking against salticids with a wide range of leg characteristics. We included S. scenicus (Fig. 8), the species studied by

Fig. 8. Salticus scenicus mature female frontal view, shows typical leg positions.

Drees (1952), in our tests, and it fell into Group B. J. queenslandicus (Group A & C), the salticid on which P. fimbriata appears to prey most frequently in nature (Fig. 9), resembles S. scenicus by having legs of more or less uniform thickness that tend to angle down at about 25° when viewed from in front. However, legs of other salticids against which P. fimbriata adopted cryptic stalking varied considerably in thickness and how they were positioned. On the whole, Drees' (1952) hypothesis would not appear to be applicable to P. fimbriata.

Body shape, along with markings on the body and appendages, are still other unlikely candidates for cues by which P. fimbriata identifies salticids, as these features varied widely among the salticids against which P. fimbriata adopted cryptic stalking. J. queenslandicus, S. scenicus and many other salticids against which P. fimbriata consistently adopted cryptic stalking have a more or less rectangular carapace when viewed from in front, and their body profiles are only moderately flat or elongated when viewed from above or the side. Other salticids against which P. fimbriata adopted cryptic stalking had more rounded frontal profiles, more elongated body profiles or more flattened bodies. Holoplatys spp. (Fig. 4a) and Mantisatta longicauda (Fig. 4b) are extreme examples, the former having dorso-ventrally compressed (flat) bodies and the latter being almost worm-like in body shape.

One characteristic shared by all prey categories against which P. fimbriata adopted cryptic stalking is a pair of large forward-facing principal eyes. By relying on the more-or-less constant shape and configuration of principal eyes across all salticid species P. fimbriata would have a reliable cue for identifying salticids. Independent of the appearance of other body parts, the principal eyes provide a cue that is unique to salticids. Arachnologists use the salticid's unique principal eyes to distinguish salticids from all other spider families (Coddington & Levi, 1991) and we suggest that P. fimbriata pays attention to much the same thing.

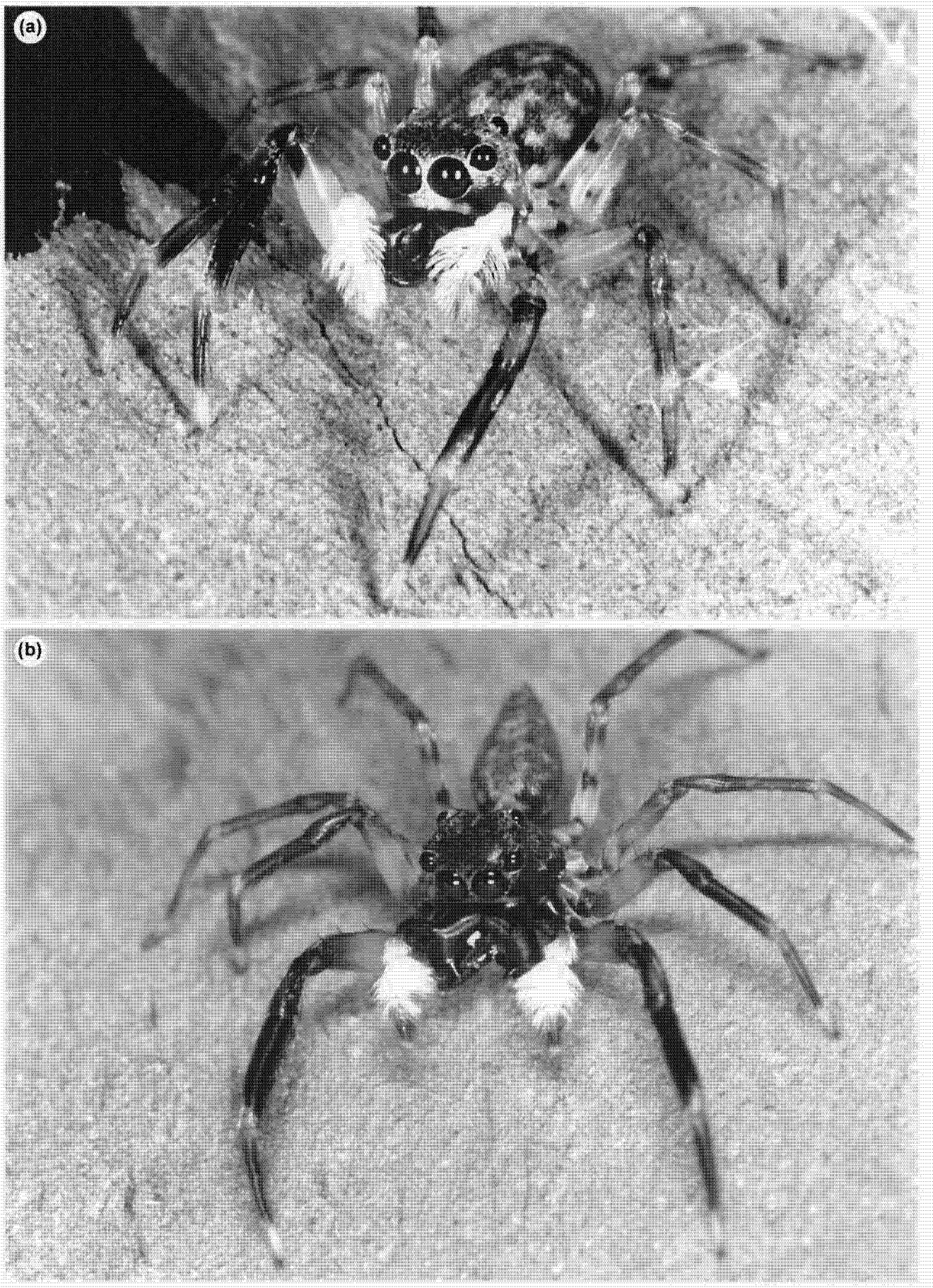

Fig. 9. Jacksonoides queenslandicus front profiles showing typical leg positions. a. Mature female. b. Mature male.

When P. fimbriata sometimes adopted cryptic stalking but other times adopted ordinary stalking (Group D salticids), this might be interpreted as instances where P. fimbriata suffered a lack of clarity about how to classify prey. Group D included the juveniles and females of A. tenuipes (Fig. 7a), G. puella, L. patens, L. viridis and O. nigrcauda. These five species are lyssomanines, and ambivalent cues from the principal eyes of these spiders may have accounted for the occasional P. fimbriata that adopted ordinary stalking. Lyssomanine females have carapaces that are highly translucent. A consequence of this is that, when viewed from the front, the principal eyes of lyssomanine females and juveniles have a flickering appearance (Fig. 10). In our study P. fimbriata never adopted ordinary stalking against males of A. tenuipes (Fig. 7b), G. puella, and L. viridis, these salticids falling into Group C instead of Group D. These lyssomanine males, in common with most salticids, have uniformly dark (non-flickering) principal eyes.

Besides lyssomanine females and juveniles, Group D included Heretemita alboplagiata (Fig. 5a), Simaethula sp. (Fig. 5b) and Sassacus papenhoei (Fig. 5c). As none of these species have translucent cuticle, and therefore all have dark principal eyes, P. fimbriata's diminished clarity at classifying these salticids would seem to be influenced by cues other than features of the principal eyes. One thing each of these three salticids has in common is being more or less beetle-like in appearance, suggesting that this is the reason for ambivalent classification. However, it does not appear to be simply a case of P. fimbriata always mistaking beetle-like salticids for real beetles. In our tests P. fimbriata never stalked, and only rarely got close to, beetles (Table 7), but beetle-like salticids were often stalked. Pachyballus cardiforme (Fig. 5d, e) from Group E (Table 5) is, at least to the human, an especially convincing beetle mimic. Almost half of the P. fimbriata tested with P. cardiforme classified it as prey (i.e., they stalked it), but only one P. fimbriata adopted cryptic stalking.

The remaining 40% of P. fimbriata that stalked P. cardiforme indicated, by adopting ambivalent stalking, that they were unable to classify this prey reliably as a salticid. These tests with beetle mimics suggest that cues other than those used by P. fimbriata to classify an arthropod as a salticid influence willingness to stalk. This would mean that, in cases where P. fimbriata did not stalk at all, we cannot strictly conclude that the arthropod was not classified as a salticid. We can only conclude that it was not classified as prey.

Evidently, a comparable argument may sometimes apply to ant mimics. Peckhamia americana (Fig. 2b) and Synageles dalmaticus are ant mimics that fell into Group E. P. fimbriata stalked these two salticids in about a third of the tests, but adopted cryptic stalking in only 20% and 8% of the tests, respectively. However, in contrast to its reaction to the beetle-like salticids, P. fimbriata appears often to classify the ant mimics as more than simply non-prey arthropods to be ignored. In contrast to how they reacted to the beetle-like P. cardiforme, most P. fimbriata that started stalking either P. americana or S. dalmaticus turned away before getting close. Myrmarachne spp. were never stalked, and P. fimbriata never got close to Myrmarachne spp.

P. fimbriata may perceive the ant mimicking salticids as chimerical freaks. As something repulsive yet strangely attractive, they probably lie outside P. fimbriata's normal classification system. Ant mimics, and beetle mimics, by providing multiple conflicting cues may be useful tools in future investigations of the perceptual hierarchy that defines P. fimbriata's prey classification system.

Fig. 10. Lyssomanes viridis mature female showing variable appearance of the large principal eyes.

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Table 1. Salticids with which *Portia fimbriata* was tested. Group A (see text): *P. fimbriata* stalked in each test and always adopted cryptic stalking.

Species	Origin	Sex/age class[a]	N	Got close[b]
Aelurillus aeruginosus (Simon)	Israel	J	26	100% (26)
Afraflacilla sp.	Kenya	F	20	100% (20)
Bagheera prosperi (G. & E. Peckham)	USA	F	20	85% (17)
Carrhotus viduus (C. L. Koch)	Sri Lanka	M	20	85% (17)
Carrhotus viduus (C. L. Koch)	Sri Lanka	F	20	100% (20)
Chalcotropis gulosa (Simon)	Philippines	F	28	71% (20)
Chalcotropis luceroi Barrion & Litsinger	Philippines	F	20	100% (20)
Chrysilla lauta Thorell	Sri Lanka	F	20	80% (16)
Cobanus unicolor Peckham	Costa Rica	M	20	65% (13)
Colopsus cancellatus Simon	Sri Lanka	M	20	100% (20)
Cytaea alburna (Keyserling)	Australia	F	22	100% (22)
Emathis weyersi Simon	Philippines	F	16	69% (11)
Eris militaris (Hentz)	USA	M	20	100% (20)
Euophrys parvula Bryant	New Zealand	M	22	86% (19)
Euryattus sp.	Australia	F	20	100% (20)
Euryattus sp.	Australia	M	20	90% (18)
Evarcha patagiata (O. P. Cambridge)	Israel	J	12	83% (10)
Evarcha sp.	Israel	J	10	100% (10)
Gedia tibialis Zabka	Singapore	F	20	95% (19)
Habrocestum pulex (Hentz)	USA	M	25	84% (21)
Harmochirus brachiatus (Thorell)	Philippines	F	20	75% (15)
Hasarius adonsoni (Audouin)	Australia	F	22	91% (20)
Heliophanus curvidens (O. P. Cambridge)	Israel	F	12	92% (11)
Heliophanus debilis Simon	Kenya	M	20	100% (20)
Heliophanus mordax (O. P. Cambridge)	Israel	F	10	100% (10)
Hentzia palmarum (Hentz)	USA	F	20	95% (19)
Jacksonoides queenslandicus Wanless	Australia	M	25	88% (22)
Metacyrba punctata (G. & E. Peckham)	Costa Rica	F	20	95% (19)
Metaphidippus exiguus (Banks)	USA	F	20	100% (20)
Metaphidippus exiguus (Banks)	USA	M	20	100% (20)
Metaphidippus felix (G. & E. Peckham)	Costa Rica	F	20	95% (19)
Mogrus dumicola (O. P. Cambridge)	Israel	J	20	100% (20)
Natta rufopicta Simon	Kenya	M	23	91% (21)
Pellenes rufoclypeata G. & E. Peckham	Kenya	F	20	100% (20)
Phidippus apacheanus Chamberlin & Gertsch	USA	J	20	90% (18)
Phidippus johnsoni (G. & E. Peckham)	USA	M	21	95% (20)
Phidippus regius C. L. Koch	USA	J	20	95% (19)
Philaeus chrysops (Poda)	Israel	J	30	93% (28)
Phintella piatensis Litsinger & Barrion	Philippines	F	23	87% (20)
Phintella vittata (C. L. Koch)	Sri Lanka	F	20	90% (18)
Piranthus casteti Simon	Sri Lanka	F	20	95% (19)
Plexippus calcutaensis (Tikader)	Australia	J	20	100% (20)
Podillothorax taprobanicus Simon	Singapore	J	27	81% (22)
Salticus tricinctus (C. L. Koch)	Israel	F	10	100% (10)
Sandolodes semicupreus (Simon)	Sri Lanka	J	20	100% (20)

Schenkelia gertschi Berland & Millot	Kenya	F	20	95% (19)
Siler semiglaucus Simon	Philippines	F	13	85% (11)
Simaetha thoracica Thorell	Australia	F	20	100% (20)
Telamonia masinloc Barrion & Litsinger	Philippines	J	11	100% (11)
Telamonia olarina Simon	Sri Lanka	F	20	100% (20)
Thiania demissa (Thorell)	Singapore	J	30	100% (30)
Thiania sp.	Philippines	J	12	100% (12)
Thorelliola ensifera (Thorell)	Singapore	M	23	100% (23)
Thyene leighi G. & E. Peckham	Kenya	J	20	85% (17)
Trite auricoma Urquhart	New Zealand	M	25	96% (24)
Trite planiceps Urquhart	New Zealand	J	30	90% (27)
Zenodorus metallescens (L. Koch)	Australia	J	10	80% (8)
Zygoballus rufipes G. & E. Peckham	USA	F	10	100% (10)

a. F = female; M = male; J = juvenile
b. Of *P. fimbriata* that 'got close' 100% used cryptic stalking when close for all salticids in the table.

Table 2. Salticids with which *Portia fimbriata* was tested. Group B (see text): *P. fimbriata* stalked in 70% or more of tests adopting only cryptic stalking.

Species	Origin	Sex/age class[a]	N	Cryptic stalk	Got close[b]
Afraflacilla sp.	Kenya	M	22	82% (18)	82% (18)
Bavia aericeps Simon	Australia	J	30	93% (28)	87% (26)
Chalcotropis gulosa (Simon)	Philippines	M	30	93% (28)	87% (26)
Chrysilla albens Dyal	Mauritius	F	11	91% (10)	73% (8)
Colopsus cancellatus Simon	Sri Lanka	F	20	95% (19)	80% (16)
Cosmophasis estrellaensis Barrion & Litsinger	Philippines	F	30	93% (28)	83% (25)
Cosmophasis estrellaensis Barrion & Litsinger	Philippines	M	30	83% (25)	83% (25)
Cytaea alburna (Keyserling)	Australia	M	22	95% (21)	82% (18)
Diolenius phrynoides Walckenaer	Australia	F	14	86% (12)	86% (12)
Epeus hawigalboguttatus Barrion & Litsinger	Philippines	J	28	89% (25)	68% (19)
Epocilla aurantica Simon	Sri Lanka	F	20	90% (18)	90% (18)
Euophrys gambosa (Simon)	Israel	J	13	85% (11)	77% (10)
Euophrys parvula Bryant	New Zealand	F	38	95% (36)	74% (28)
Frigga pratenus (G. & E. Peckham)	Costa Rica	F	20	95% (19)	75% (15)
Habrocestum pulex (Hentz)	USA	F	25	88% (22)	72% (18)
Heliophanillus fulgens (O. P. Cambridge)	Israel	F	11	91% (10)	91% (10)
Heliophanus debilis Simon	Kenya	F	20	90% (18)	65% (13)
Hentzia mitrata (Hentz)	USA	F	20	90% (18)	85% (17)
Hypaeus cucullatus Simon	Costa Rica	F	20	90% (18)	80% (16)
Hypaeus cucullatus Simon	Costa Rica	M	20	90% (18)	85% (17)
Icius sp.	Philippines	F	15	87% (13)	67% (10)
Lagnus sp.	Philippines	J	15	93% (14)	80% (12)
Langona oreni Proszynski	Israel	J	20	85% (17)	80% (16)
Langona redii (Savigny & Audouin)	Israel	J	12	92% (11)	92% (11)
Lepidemathis sericea (Simon)	Philippines	F	15	80% (12)	67% (10)
Marpissa marina Goyen	New Zealand	F	22	91% (20)	77% (17)
Mopsus mormon Karsch	Australia	J	25	96% (24)	96% (24)
Ocrisiona complanata L. Koch	Australia	J	20	85% (17)	75% (15)

Orthrus bicolor Simon	Philippines	M	14	86% (12)	79% (11)
Pellenes rufoclypeata G. & E. Peckham	Kenya	M	20	95% (19)	85% (17)
Phidippus johnsoni (G. & E. Peckham)	USA	J	28	90% (25)	86% (24)
Phidippus otiosus (Hentz)	USA	J	20	85% (17)	70% (14)
Phintella piatensis Litsinger & Barrion	Philippines	M	20	90% (18)	80% (16)
Phlegra particeps (O.P. Cambridge)	Israel	J	12	92% (11)	92% (11)
Salticus scenicus (Clerck)	U.K.	F	20	90% (19)	90% (19)
Sandolodes ludicrus (Keyserling)	Australia	J	24	83% (20)	79% (19)
Servea vestita (L. Koch)	Australia	J	20	84% (17)	84% (17)
Simaetha paetula (Keyserling)	Australia	M	22	86% (19)	79% (15)
Simaetha thoracica Thorell	Australia	M	20	80% (16)	65% (13)
Thianitara sp.	Philippines	F	16	94% (15)	81% (13)
Thiodina sylvana Hentz	USA	F	25	88% (22)	84% (21)
Thorelliola ensifera (Thorell)	Singapore	F	23	91% (21)	87% (20)
Thyene imperialis (Rossi)	Israel	J	11	91% (10)	82% (9)
Trite auricoma Urquhart	New Zealand	F	28	96% (27)	96% (27)
Tularosa plumosa de Lessert	Kenya	F	20	90% (18)	90% (18)
Tularosa plumosa de Lessert	Kenya	M	20	70% (14)	70% (14)
Viciria praemandibularis (Hasselt)	Singapore	J	24	79% (19)	75% (18)
Xenocytaea sp.	Philippines	F	18	94% (17)	78% (14)

a. F = female; M = male; J = juvenile
b. Of *P. fimbriata* that 'got close' 100% used cryptic stalking when close for all salticids in the table.

Table 3. Salticids with which *Portia fimbriata* was tested. Group C (see text): *P. fimbriata* adopted both ambivalent and cryptic stalking.

Species	Origin	Sex/age class[a]	N	Cryptic stalk	Ambivalent stalk	Got close[b]
Asemonea murphyae Wanless	Kenya	F	14	57% (8)	7% (1)	36% (5)
Asemonea murphyae Wanless	Kenya	M	12	67% (8)	8% (1)	33% (4)
Asemonea tenuipes O. P. Cambridge	Sri Lanka	M	20	60% (16)	10% (2)	55% (11)
Blaisea bicalcurata Simon	Kenya	F	20	85% (17)	5% (1)	70% (14)
Cobanus unicolor Peckham	Costa Rica	F	20	85% (17)	15% (3)	60% (12)
Corythalia canosa (Walckenaer)	USA	F	22	91% (20)	9% (2)	86% (19)
Cosmophasis micarioides (L. Koch)	Australia	F	26	81% (21)	9% (2)	73% (19)
Cosmophasis modestus (Keyserling)	Australia	F	23	87% (20)	9% (2)	70% (16)
Cyrba ocellata (Kroneburg)	Kenya	F	11	82% (9)	9% (1)	64% (7)
Epeus sp. 1	Singapore	J	25	96% (24)	4% (1)	84% (21)
Eris militaris (Hentz)	USA	F	20	80% (16)	10% (2)	70% (14)
Frigga pratenus (G. & E. Peckham)	Costa Rica	M	20	80% (16)	5% (1)	80% (16)
Gambaquezonia itimana Barrion & Litsinger	Philippines	J	15	87% (13)	7% (1)	73% (11)
Goleba puella (Simon)	Kenya	M	20	80% (16)	10% (2)	50% (10)
Hasarius adonsoni (Audouin)	Australia	M	20	85% (17)	10% (2)	70% (14)
Helpis minitabunda (L. Koch)	Australia	J	24	92% (18)	8% (2)	63% (15)
Heretemita alboplagiata (Simon)	Philippines	F	30	87% (26)	7% (2)	67% (20)
Holoplatys sp. 1	New Zealand	F	28	93% (26)	7% (2)	54% (15)
Hyllus dotatus (G. & E. Peckham)	Kenya	F	20	75% (15)	10% (2)	60% (12)
Jacksonoides queenslandicus Wanless	Australia	F	52	92% (48)	4% (2)	81% (42)
Lyssomanes viridis (Walckenaer)	USA	M	21	71% (15)	10% (2)	67% (14)
Mantisatta longicauda Cutler & Wanless	Philippines	M	30	77% (23)	10% (3)	70% (21)

Mantisatta longicauda Cutler & Wanless	Philippines	F	35	57% (20)	6% (2)	54% (19)
Marengo marina Goyen	Malaysia	F	20	85% (17)	10% (2)	75% (15)
Marpissa marina Goyen	New Zealand	M	22	82% (18)	9% (2)	64% (14)
Menemerus bivittatus (Dufour)	Queensland	J	28	83% (23)	7% (2)	75% (21)
Natta rufopicta Simon	Kenya	F	26	81% (21)	4% (1)	73% (19)
Orthrus bicolor Simon	Philippines	F	14	71% (10)	14% (2)	64% (9)
Philaeus sinilis Denis	Kenya	F	20	80% (16)	5% (1)	65% (13)
Philaeus sinilis Denis	Kenya	M	20	90% (18)	5% (1)	75% (15)
Platycryptus undata (DeGeer)	USA	J	26	88% (23)	12% (3)	77% (20)
Plexippus paykulli (Savigny & Audouin)	USA	J	30	83% (25)	7% (2)	83% (25)
Ptocasius sp.	Singapore	F	20	80% (16)	5% (1)	75% (15)
Rhene sp.	Malaysia	F	21	81% (17)	10% (2)	71% (15)
Siler semiglaucus Simon	Sri Lanka	F	20	70% (14)	5% (1)	60% (12)
Simaetha paetula (Keyserling)	Australia	F	26	77% (20)	8% (2)	69% (18)
Thiodina sylvana Hentz	USA	M	25	80% (20)	4% (1)	72% (18)
Zenodorus oribiculatus (Keyserling)	Australia	F	25	80% (20)	4% (1)	76% (19)

a. F = female; M = male; J = juvenile
b. Of *P. fimbriata* that 'got close' 100% used cryptic stalking when close for all salticids in the table.

Table 4. Salticids with which *Portia fimbriata* was tested. Group D (see text): *P. fimbriata* adopted ordinary stalking and cryptic stalking.

Species	Origin	Sex/age class[a]	N	Cryptic stalk	Ordinary stalk	Ambivalent stalk	Got close[b]
Asemonea tenuipes O. P. Cambridge	Sri Lanka	F	22	73% (16)	9% (2)	9% (2)	45% (10)
Cyrba algerina (Lucas)	Portugal	F	25	80% (20)	5% (1)	5% (1)	68% (17)
Goleba puella (Simon)	Kenya	F	20	50% (10)	5% (1)	15% (3)	35% (7)
Holoplatys planissimus (L. Koch)	New Zealand	J	30	83% (25)	3% (1)	7% (2)	63% (19)
Heretemita alboplagiata (Simon)	Philippines	M	30	73% (22)	7% (2)	7% (2)	40% (12)
Lyssomanes patens (G. & E. Peckham)	Costa Rica	J	10	70% (7)	10% (1)	20% (2)	60% (6)
Lyssomanes viridis (Walckenaer)	USA	F	52	88% (46)	2% (1)	8% (4)	79% (41)
Marengo sp.	Kenya	F	17	71% (12)	12% (2)	6% (1)	53% (9)
Marengo crassipes (G. & E. Peckham)	Sri Lanka	F	20	75% (15)	10% (2)	0	55% (11)
Mopsus mormon Karsch	Australia	M	22	86% (19)	5% (1)	0	73% (16)
Onomastus nigricauda L. Koch	Sri Lanka	F	20	55% (11)	15% (3)	5% (1)	55% (11)
Sassacus papenhoei G. & E. Peckham	USA	F	28	68% (19)	7% (2)	7% (2)	68% (19)
Simaethula sp.	Australia	F	23	85% (17)	4% (1)	4% (1)	70% (16)
Thiania bhamoensis Thorell	Singapore	J	20	85% (17)	5% (1)	0	80% (16)

a. F = female; M = male; J = juvenile
b. Of *P. fimbriata* that 'got close' 100% used cryptic stalking when close for all salticids in the table, except for *Sassacus papenhoei* for which 95% (all but one) used cryptic stalking when close.

Table 5. Salticids with which *Portia fimbriata* was tested. Group E (see text): *P. fimbriata* adopted relatively low levels of cryptic stalking.

Species[a]	Origin	N	Cryptic stalk	Ordinary stalk	Ambivalent stalk	Got close	Cryptic stalk when close
Pachyballus cardiforme Berland & Millot	Kenya	15	7% (1)	0	40% (6)	33% (5)	40% (2)
Peckhamia americana (G. & E. Peckham)	USA	25	20% (5)	4% (1)	8% (2)	4% (1)	100% (1)
Synageles dalmaticus (Keyserling)	Israel	12	8% (1)	0	25% (3)	8% (1)	0

a. All adult females.

Table 6. Ant-mimic salticids from genus *Myrmarachne* with which *Portia fimbriata* was tested.

Species	Origin	Sex/age class[a]	N	Got close[b]
Myrmarachne assimilis Banks	Philippines	F	40	5% (2)
Myrmarachne assimilis Banks	Philippines	M	28	0
Myrmarachne bakeri Banks	Philippines	F	30	0
Myrmarachne bakeri Banks	Philippines	M	20	0
Myrmarachne bellicosa (G. & E. Peckham)	Philippines	F	20	5% (1)
Myrmarachne bellicosa (G. & E. Peckham)	Philippines	M	20	0
Myrmarachne bidentata Banks	Philippines	F	20	0
Myrmarachne bidentata Banks	Philippines	M	20	0
Myrmarachne elongata Szombathy	Sri Lanka	F	20	0
Myrmarachne elongata Szombathy	Sri Lanka	M	20	10% (2)
Myrmarachne gedongensis Badcock	Sri Lanka	F	20	0
Myrmarachne gigantea Zabka	Singapore	M	20	0
Myrmarachne giltayi Roewer	Kenya	F	20	0
Myrmarachne kiboschensis de Lessert	Kenya	F	20	0
Myrmarachne kiboschensis de Lessert	Kenya	M	20	5% (1)
Myrmarachne kilifi Wanless	Kenya	F	26	4% (1)
Myrmarachne kilifi Wanless	Kenya	M	20	10% (2)
Myrmarachne laurentina Bacelar	Sri Lanka	F	20	5% (1)
Myrmarachne lawrenci Roewer	Kenya	F	20	0
Myrmarachne luctuosa (L. Koch)	Australia	F	25	0
Myrmarachne lupata L. Koch	Australia	F	35	11% (4)
Myrmarachne lupata L. Koch	Australia	M	26	0
Myrmarachne marshalli G. & E. Peckham	Sri Lanka	F	20	5% (1)
Myrmarachne marshalli G. & E. Peckham	Sri Lanka	M	20	10% (2)
Myrmarachne maxillosa (L. Koch)	Singapore	F	20	0
Myrmarachne maxillosa (L. Koch)	Singapore	M	20	0
Myrmarachne melanocephala MacLeay	Sri Lanka	F	38	5% (2)
Myrmarachne melanocephala MacLeay	Sri Lanka	M	20	0
Myrmarachne militaris Szombathy	Kenya	F	28	0
Myrmarachne militaris Szombathy	Kenya	M	20	5% (1)
Myrmarachne naro Wanless	Kenya	F	28	5% (1)
Myrmarachne naro Wanless	Kenya	M	22	0
Myrmarachne nigella Simon	Philippines	F	20	0
Myrmarachne providens G. & E. Peckham	Sri Lanka	F	20	0
Myrmarachne providens G. & E. Peckham	Sri Lanka	M	20	15% (3)
Myrmarachne richardsi Wanless	Kenya	F	20	0
Myrmarachne richardsi Wanless	Kenya	M	20	0
Myrmarachne uvira Wanless	Kenya	F	20	0
Myrmarachne uvira Wanless	Kenya	M	20	10% (2)

a. F = female; M = male

b. No *P. fimbriata* stalked any salticid in this table.

Table 7. Non-salticid spiders and insects presented to *Portia fimbriata* during tests.

Species	Description	Origin	Order/Family	Sex/age class[a]	N	Stalked[b]	Got close
Lycosa hilaris L. Koch	Wolf spider	New Zealand	Araneae/Lycosidae	J	20	60% (12)	65% (13)
Lycosa hilaris L. Koch	Wolf spider with eggs	New Zealand	Araneae/Lycosidae	F	20	50% (10)	55% (11)
Clubiona cambridgei (L. Koch)	Hunting spider	New Zealand	Araneae/Clubionidae	J	30	0	0
Achaearanea sp.	Web-building spider	New Zealand	Araneae/Theridiidae	F	20	90% (18)	90% (18)
Badumna longinquus (L. Koch)	Web-building spider	New Zealand	Araneae/Desidae	J	20	75% (15)	55% (11)
Drosophila melanogaster Meigen	Fruit fly	Culture	Diptera/Drosophilidae	A	20	25% (5)	10% (2)
Musca domestica Linnaeus	House fly	Culture	Diptera/Muscidae	A	20	35% (7)	35% (7)
Monomorium antarcticum (White)	Ant (worker)	New Zealand	Hymenoptera/ Formicidae	F	30	0	7% (2)
Oecophylla smaragdina (Fabicius)	Ant (worker)	Queensland	Hymenoptera/ Formicinae	A	16	0	0
Polyrachis sp.	Ant (worker)	Queensland	Hymenoptera/ Formicinae	A	12	0	0
Tapinoma sp.	Ant (worker)	Queensland	Hymenoptera/ Dolichoderinae	A	14	0	7% (1)
Coccinella undecimpunctata Linnaeus	11 spotted lady bird beetle	New Zealand	Coleoptera/ Coccinellidae	A	16	0	0
Exapion ulicis (Forster)	Seed weevil	New Zealand	Coleoptera/Brentitidae (Apioninae)	A	15	0	0
Paropsis charybdis Stål	Eucalyptus tortoise beetle	New Zealand	Coleoptera/ Chrysomelidae	A	15	0	7% (1)
Unknown	Fire fly beetle	Queensland	Coleoptera/ Lampyridae	A	12	0	0
Unknown	Net-winged beetle	Queensland	Coleoptera/Lycidae	A	12	0	8% (1)
Unknown	Tumbling flower beetle	Queensland	Coleoptera/ Mordellidae	A	12	0	0

a. F = female; J = juvenile; A = adult
b. All stalking of non-salticids was ordinary stalking, even when close. However, there were two cases (10%) of ambivalent stalking of *Lycosa hilaris* without eggs and one (5%) of *L. hilaris* with eggs.

Chapter 6.

This chapter has been submitted to the *Journal of Experimental Biology*. The text is presented here in the same format as the submitted manuscript. Figures and their captions have been placed close to where they are referenced in the text and tables follow the text.

CUES BY WHICH *PORTIA FIMBRIATA*, AN ARANEOPHAGIC JUMPING SPIDER, DISTINGUISHES JUMPING-SPIDER PREY FROM OTHER PREY

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SUMMARY

Portia fimbriata from Queensland, Australia, is an araneophagic jumping spider (Salticidae) that includes in its predatory strategy a tactic (cryptic stalking) enabling it to prey effectively on a wide range of salticids from other genera. Optical cues used by P. fimbriata to identify the salticid species on which it most commonly preys were investigated experimentally in the laboratory using odourless lures made from dead prey on which various combinations of features were altered. P. fimbriata adopted cryptic stalking only against intact salticid lures and modified lures on which the large anterio-medial eyes were visible. Ordinary stalking was usually adopted when the lure did not have the anterio-medial eyes visible. There was no evidence that cues from the legs of prey salticids influence P. fimbriata's choice of stalking style, but cues from legs do appear to influence strongly whether a prey is stalked at all. Cues from the cephalothorax and abdomen also influenced stalking tendency, but to a lesser degree than cues from the legs. An algorithm to describe P. fimbriata's perceptual processes when visually discriminating between salticid and non-salticid prey is discussed.

Introduction

Jumping spiders (Salticidae) have exceptional eyes (Land, 1985a; Blest, 1987). Three pairs positioned along the sides of the cephalothorax (called the 'secondary eyes') have a combined field-of-view close to 360° and serve primarily as movement detectors (Land, 1971, 1985b). A pair of forward-facing anterior medial eyes (called the 'principal eyes') are adapted for colour vision and high spatial acuity (Blest et al., 1981; Blest and Price, 1984).

Salticids also have exceptionally intricate predatory strategies. Although a minority of species is araneophagic (eat primarily other spiders), motile insects are the primary prey of most salticids. Prey capture tends to be largely, but not entirely (Taylor et al., 1998), guided by vision (Forster, 1982), eyesight alone enabling the salticid to disinguish rapidly between prey, conspecific rivals and potential mates. Use of different prey-capture tactics against different types of prey ('predatory versatility': Curio, 1976) may be widespread (Edwards and Jackson, 1993), and is especially pronounced in myrmecophagic (ant eating) and araneophagic species (Li and Jackson, 1996a). Using vision alone, myrmecophagic and araneophagic salticids are able to discriminate between different types of prey (Li and Jackson, 1996b; Li et al. 1999), but there is little precise information about the optical cues relied upon by these species.

Among the araneophagic salticids, Portia spp. have particularly complex predatory strategies. These species are unusual because, in addition to stalking prey away from webs, they build prey-capture webs of their own and invade webs of other spiders, against which they adopt predatory tactics based on aggressive mimicry (Jackson and Wilcox, 1998). Among species and populations of Portia studied, the Queensland P. fimbriata appears to be unique because its preferred prey are other genera of salticids (Li and Jackson, 1996b). Aggressive-mimicry signals are used to entice nesting salticids out of their nests, and a

special tactic, cryptic stalking, is used for capturing salticids in the open, away from nests and webs (Jackson and Blest, 1982).

Portia does not look like a typical salticid - nor even an animal. In a web, it resembles a piece of detritus (Wanless, 1978), and when walking, its slow, choppy gait is unlike that of any other salticid. When resting in a web, Portia adopts a special posture, called the 'cryptic rest posture', by pulling legs in close to the body and its palps back beside the chelicerae (Jackson and Blest, 1982). When cryptic stalking, the Queensland P. fimbriata holds its palps retracted beside its chelicerae, as in the cryptic rest posture, and exaggerates the slow, choppy gait of its normal locomotion. If faced by its salticid prey, P. fimbriata freezes until the prey turns away. Cryptic stalking can be easily distinguished from 'ordinary' stalking because, when stalking any type of prey other than salticids, P. fimbriata does not consistently pull its palps back, nor does it freeze when faced. Most salticids fail to recognize a cryptically stalking Queensland P. fimbriata as a predator, but they often defend themselves when stalked by other species of Portia or by P. fimbriata from sites other than Queensland (Jackson and Hallas, 1986).

Salticids are especially abundant in the habitat of the Queensland Portia, and cryptic stalking appears to be a local adaptation to these locally abundant prey (Jackson and Blest, 1982). Although many species of salticids are found in the Queensland rain forest, one species, Jacksonoides queenslandicus, appears to be by far the most abundant on the tree trunks, boulders and rock walls in the microhabitat of P. fimbriata (Jackson, 1988). The disproportionate abundance of J. queenslandicus within P. fimbriata's environment suggests that J. queenslandicus, rather than salticids in general, might have been responsible for the evolution of cryptic stalking.

However, the cues that trigger cryptic stalking are not specific to J. queenslandicus. Using standardised tests in which only optical cues were available (prey enclosed in small glass vial within large cage), P. fimbriatas' reactions to 114 salticid species were investigated in an earlier study (Harland and Jackson, in prep). Not only sympatric, but also allopatric, salticids were tested, and species with considerably different appearance were tested, including beetle mimics, species with unusual body shapes, and species with a wide variety of camouflaging markings. Except for Myrmarachne spp. (ant mimics), all salticids tested triggered cryptic stalking by P. fimbriata. This suggests that some features common to most salticids act as cues that elicits cryptic stalking by P. fimbriata, but experimental studies are needed for clarifying what these cues may be.

Experiments using odourless lures made from dead, dried prey coated with a plastic lacquer (aerosol spray), mounted in life-like postures and presented without movement, have confirmed that movement patterns are not necessary. Static cues from appendages, body shape and other features (called here after 'body form' for short) apparently suffice to enable Queensland P. fimbriata to distinguish salticids from other types of spiders and from insects (Jackson and Tarsitano, 1993; Li and Jackson, 1996b).

Using lures made from intact females of J. queenslandicus as a standard, and systematically altering the appearance of otherwise life-like lures, we investigate here the potential significance as cryptic-stalking cues of specific features of the salticid body form.

Materials and methods

Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier spider studies (Jackson and Hallas, 1986). Testing was carried out between 0900 h and 1700 h (laboratory photoperiod 12L:12D, lights on at 0800).

Each P. fimbriata tested was either a juvenile (4-8 mm in body length) or an adult female (8-10 mm body length) and no individual P. fimbriata was used in more than one test. Individuals of P. fimbriata were chosen at random from the stock culture for each specific test. No adult or subadult (one instar previous to maturity) males were tested. All P. fimbriata tested were reared from eggs in the laboratory, and none had prior contact with salticids of any species other than with conspecifics in the eggsac before dispersal. Hunger state was standardized before testing by keeping each P. fimbriata without prey for 5 days.

Lures were presented to P. fimbriata on a wooden ramp (300 mm long and 70 mm wide, raised at a 20° incline) supported by two wooden poles (diameter 20 mm) glued to a wooden base (400 mm long and 100 mm wide) (Fig. 1). The ramp and the base were both 17 mm thick. The two poles were situated 75 mm and 150 mm, respectively, from the upper end of the base. The entire apparatus was painted with two coats of water-resistant polyurethane. As a precaution against possible chemical traces left by previously tested P. fimbriata, the ramp was wiped off with 80% ethanol, then allowed to dry for at least 30 min, between each test.

A piece of brown cardboard (80 mm high and 70 mm wide) glued to the top end of the ramp served as a background against which the salticid saw the lure. A lure (on a cork disk) was placed on a spring loaded platform within a hole drilled through the surface of the ramp (diameter 15 mm) and centred 40 mm from the base of the cardboard. Standardized movement of the lure was generated by a switch operated device below the platform (Fig. 1) which was activated automatically at 10-sec intervals. At rest the lure sat level with the rampsurface. Activating the switch released a spring, causing the lure to jump 5 mm above the level of the ramp surface, after which a motor slowly pulled the lure back to the rest

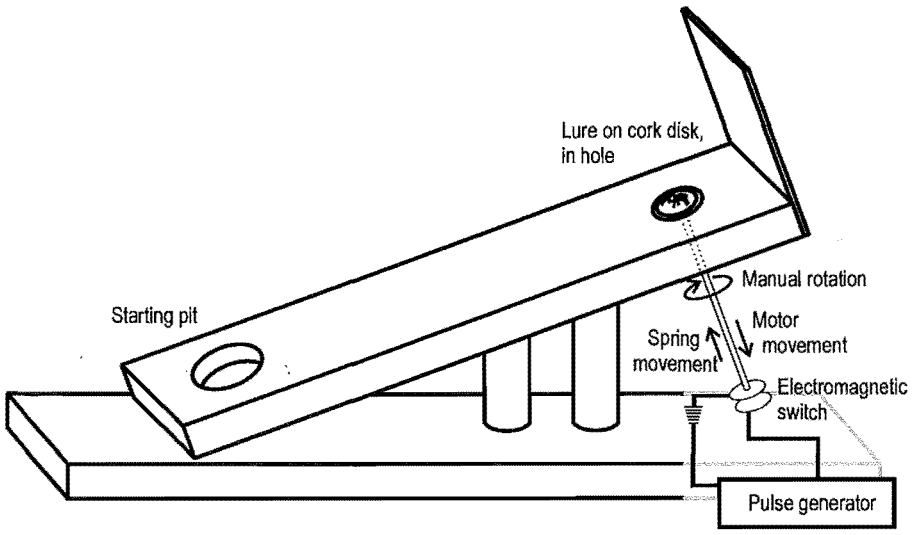

Fig. 1. Testing ramp for presenting lures to Portia fimbriata. At beginning of test, P. fimbriata climbs out of starting pit and walks up incline. Every 10 s, pulse generator releases electromagnetic switch and causes lure to spring above ramp surface by 5 mm. An electric motor pulls lure slowly back to level with ramp surface, resetting electromagnetic switch. Lure initially faces 45° from starting pit but is turned to face P. fimbriata when P. fimbriata closes to within 50 mm. Test ends 15 s later.

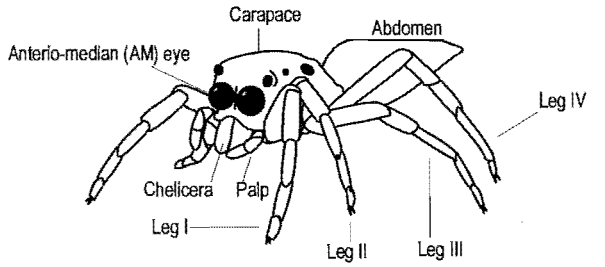

Fig 2. Conventions for naming body parts on Jacksonoides queenslandicus.

position (cycle duration ~1 sec). Movement attracted P. fimbriata's attention to the lure and ensured that P. fimbriata remained attentive to the lure while ascending of the ramp.

Before each test, a P. fimbriata was placed in a pit (diameter 32 mm, depth 10 mm, centred 60 mm from the bottom of the ramp) drilled into the top surface of the ramp 200 mm from the lure. The pit was covered with a piece of glass until P. fimbriata became quiescent, then uncovered to start a test (test began when P. fimbriata walked slowly out of the pit and onto the ramp). P. fimbriata tends to walk up inclines and usually ascended toward the lure after leaving the pit. Lighting was from a 100 watt tungsten filament lamp bulb 0.75 m above the ramp and fluorescent tube ceiling lights 2 m above the ramp (approx. 1850 lux at ramp surface).

At the beginning of a test, the lure faced 45° from the pit and the emerging P. fimbriata. The lure could be rotated by hand. When P. fimbriata came to within 50 mm, the lure's orientation was adjusted by suddenly rotating it to face P. fimbriata. After observing P. fimbriata's reaction for the next 15 sec, the test ended.

'Stalking' was defined as steady head-on movement toward a lure. Three categories were recognized: cryptic stalking (consistent adoption of the retracted-palps posture and freezing when a lure no more than 50 mm away was facing); ordinary stalking (consistent adoption of the same posture used during ordinary locomotion, including holding the palps loosely in front of the chelicerae, and failure to freeze when faced by a lure that was 50 mm or closer); ambivalent stalking (test spiders sometimes adopted the retracted-palps posture or sometimes froze when faced by the lure when no more than 50 mm away, but failed to do so consistently). Spiders that reached the top of the ramp without stalking the lure were recorded as not responding. Data on stalking style and tendency to stalk (i.e., pursuit tendency) were

analysed. Results from using different lures were compared (tests of independence with Bonferonni adjustments).

Intact lures (controls) were made, as in previous studies (Jackson and Tarsitano, 1993; Li and Jackson, 1996b), by mounting dead, dried prey on cork disks. Experimental lures were made by systematically modifying the appearance of intact lures (Fig. 2). A total of 18 different lures were tested (Fig. 3). Lures made from an intact salticid (J. queenslandicus Wanless; Fig. 3a), an intact wolf spider (Lycosa hilaris Forster; Fig. 3b) and an intact house fly (Musca domesticus Linnaeus; Fig. 3c) provided a basis for comparing P. fimbriata's reactions to 15 modified lures (Fig. 3d-r).

Influence of the presence of legs and palps

Methods

Eight modified lures were made by removing combinations of legs, palps or both from intact salticid lures: two palps removed (Fig. 3d); one leg I removed (Fig. 3e); both legs I removed (Fig. 3f); four legs (pairs I and II) removed (Fig. 3g); both legs II removed (Fig. 3h); four legs (I and II), and both palps removed (Fig. 3i); all legs removed (Fig. 3j); all appendages (8 legs and 2 palps) removed (Fig. 3k).

Results

When data from using an intact salticid lure were compared with data from using each of the modified lures, there were no significant differences in how often different stalking styles were adopted by P. fimbriata (Table 1). Pursuit tendencies against the lure with both palps removed, the lure with a single leg I removed and the lure with both legs II removed were not significantly different from the pursuit tendency against the intact salticid lure (Fig. 4a).

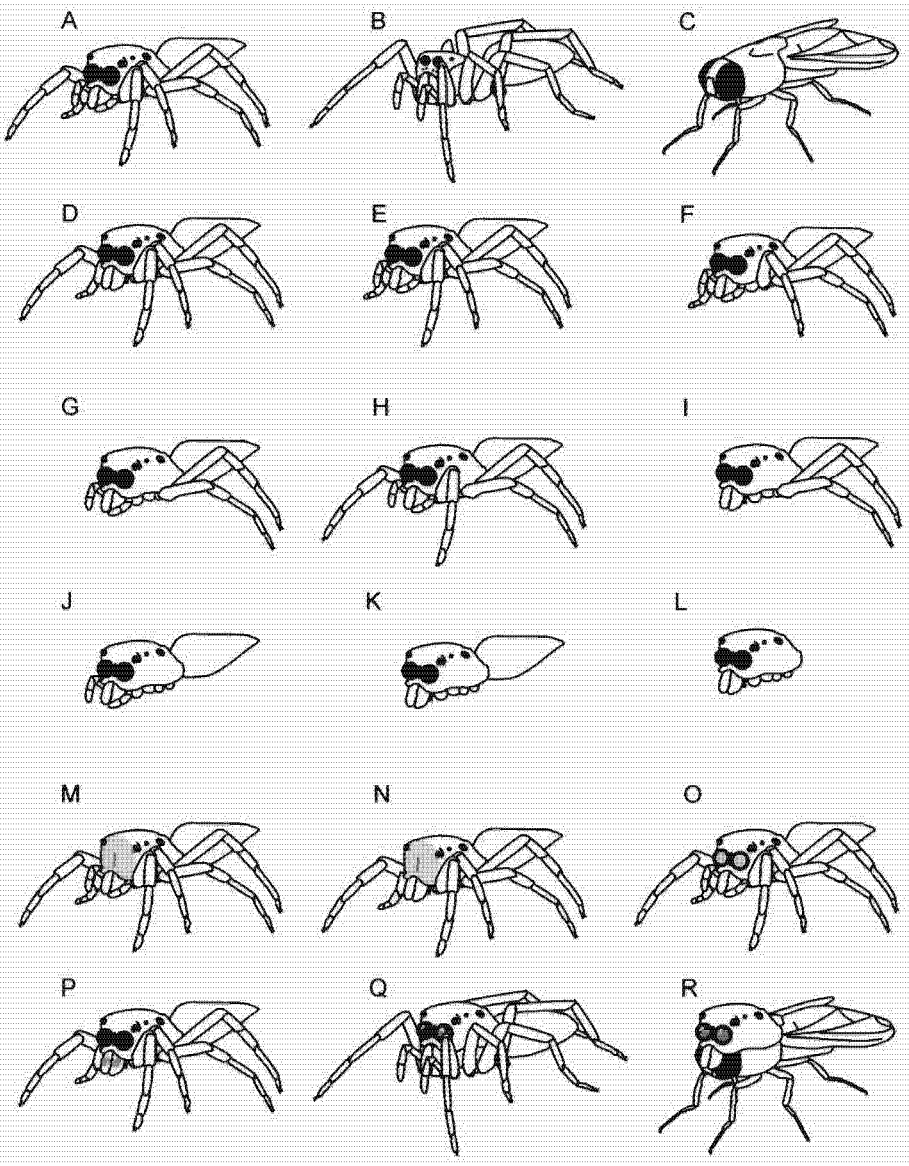

Fig 3. Lures used to test for optical cues that trigger cryptic stalking by Portia fimbriata. Intact lures made from (A), Jacksonoides queenslandicus, (B), Lycosa hilaris (wolf spider) and (C), Musca domesticus (house fly). Modified lures made from J. queenslandicus with: (D), palps removed; (E), one leg I removed; (F), both legs I removed; (G), legs I and II removed; (H), legs II removed; (I), legs I, legs II and palps removed; (J), all legs removed; (K), all legs and palps removed; (L), legs, palps, and abdomen removed; (M), AM eyes painted over (outlines obliterated); (N), AM eyes painted over and palps removed; (O), AM eyes painted over, but leaving outlines intact; (P), circles painted on chelicerae and palps removed. Two modified non-salticid lures: J. queenslandicus carapaces (semi-transparent AM eyes) mounted over the anterior dorsal regions of , (Q), L. hilaris and (R), M. domesticus.

However, compared with the intact salticid lure, significantly fewer P. fimbriata stalked each of the other modified lures (Fig. 4b-c).

Influence of the presence of an abdomen

Methods

Two salticid lures were used to test whether the presence of an abdomen is a cue. One lure (Fig. 3k) had all of its legs and its palps removed, but the abdomen was left intact. The other lure was the same except that its abdomen was also removed (Fig. 3l). Removing the legs and palps from both lures ensured that the abdomen (or its absence) was clearly visible, rather than being partly or wholly occluded by appendages.

Results

Comparing data from testing with each of the modified lures and data from testing with the intact lure, there was no significant difference in the frequency with which different stalking styles were adopted by P. fimbriata. However, significantly more P. fimbriata (Table 1) stalked the intact lure and the lure with no legs or palps (but the abdomen intact) than stalked the lure with no abdomen (Fig. 4c).

Influence of the presence of a salticid carapace

Methods

Three intact lures (salticid, lycosid and house fly) and three modified lures were used (Fig. 3). One modified lure had all of the legs, both of the palps and the abdomen removed (Fig. 3l), leaving the cephalothorax alone. The remaining two modified lures were made from an intact lycosid and an intact fly onto which an excised J. queenslandicus carapace, with chelicerae

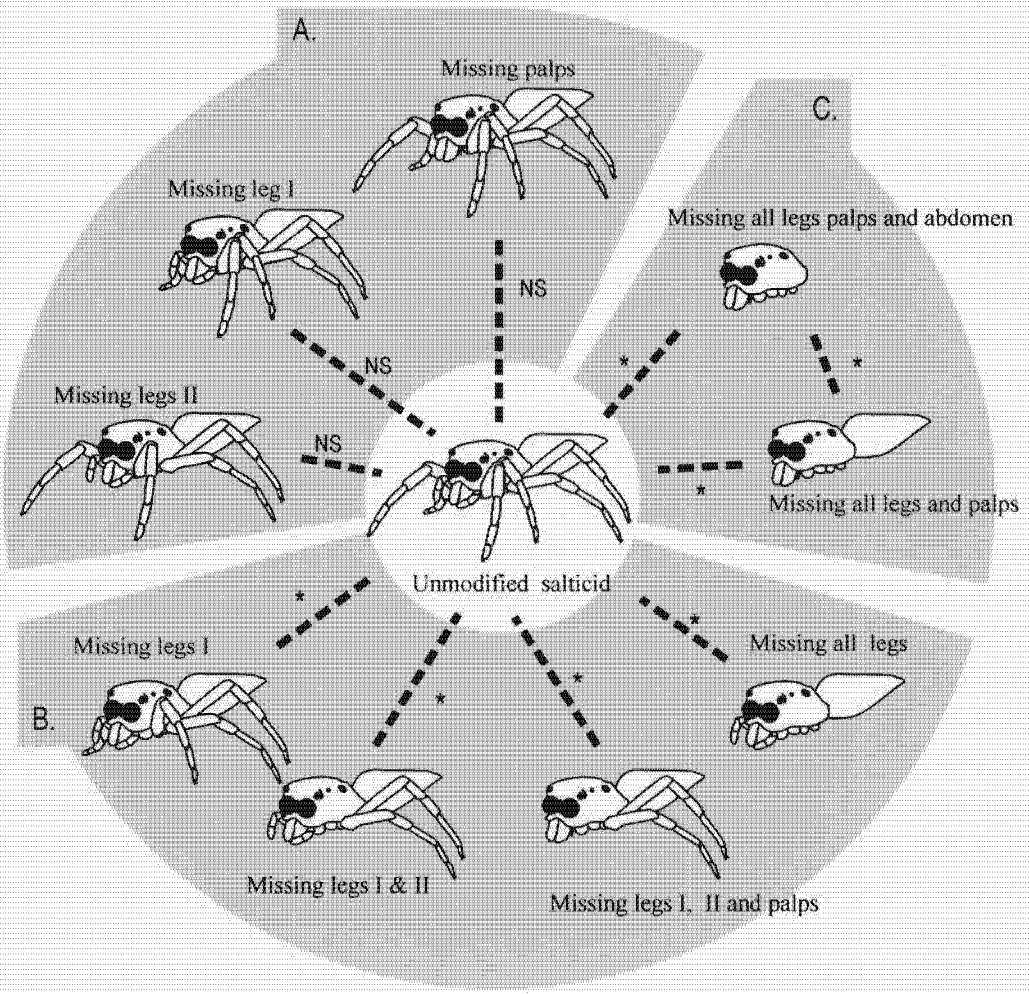

Fig 4. Comparisons (chi-square tests of independence with Bonferoni adjustments) of Portia fimbriata's tendency to stalk intact and modified J. queenslandicus lures (different combinations appendages removed). (A) Between three modified lures and intact lure there was no significant difference in stalking tendency. (B, C) For six lures, stalking tendency was significantly lower than with intact lure. (C) Abdomen's influence on P. fimbriata's stalking tendency shown by comparing lures with all appendages removed and lures with abdomen also removed.

intact, was glued (over the lycosid's own carapace and over the dorsal region of the head and thorax of the fly): called the 'lycosid-salticid' (Fig. 3q) and 'fly-salticid' (Fig. 3r) lures, respectively. Although the lycosid-salticid and fly-salticid lures had non-salticid legs and body parts, they had salticid carapaces with large AM eyes. The AM eyes, being hollow, were nearly transparent.

Results

When data from using an intact salticid lure were compared with data from using the three modified lures that retained a salticid carapace (isolated salticid cephalothorax, lycosid-salticid and fly-salticid), there was no significant difference in how often different stalking styles were adopted by P. fimbriata (Table 1). However, there was a significant difference in how often different stalking styles were adopted with the intact house-fly lure and the intact lycosid lure compared with the intact salticid lure, the lycosid-salticid lure and the fly-salticid lure (Fig. 5).

Pursuit tendency against the intact lycosid lure and the lycosid-salticid lure were not significantly different from the pursuit tendency against the intact lure (Fig. 5). Neither was there a significant difference between the pursuit tendency against the fly-salticid lure and the intact house-fly lure, nor against the lycosid-salticid lure and the intact lycosid lure. However, compared with the intact salticid lure, significantly fewer P. fimbriata stalked the isolated salticid cephalothorax, the intact house-fly lure and the fly-salticid lure.

Influence of the anterio-median eyes

Methods

Four salticid lures were designed. Using a fine brush, paint (opaque, red, water-based enamel) was applied to the anterior surfaces of the carapaces (faces) of two lures (one with palps

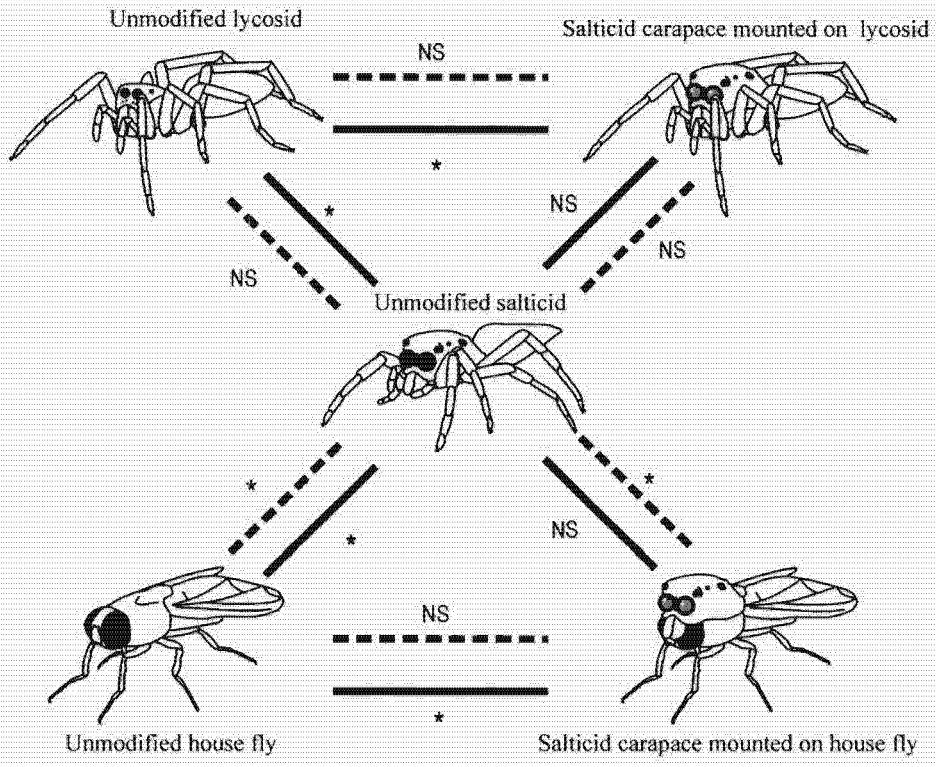

Fig. 5. Comparisons (chi-square test of independence with Bonferoni adjustment) showing influence of salticid carapace on Portia fimbriata's stalking tendency (dashed lines) and stalking style (solid lines).

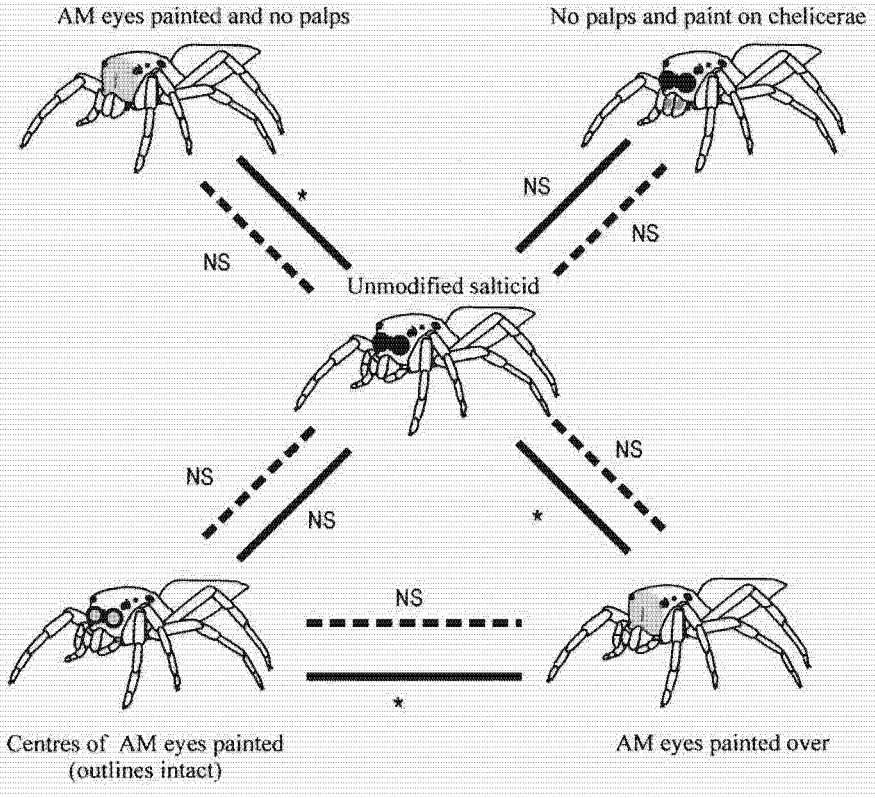

Fig. 6. Comparisons (chi-square test of independence with Bonferoni adjustment) showing influence of salticid AM eyes on Portia fimbriata's stalking tendency (dashed lines) and stalking style (solid lines).

removed and the other intact), completely obscuring all details of the AM eyes (Fig. 3m-n). Another two lures were controls for effects of the paint. One had paint carefully applied to the lens of each AM eye, coating the surface but leaving the outline intact (Fig. 3o). The other control lure (palps removed) had a circle of paint, approximately the same size as an AM eye, applied to the anterior of the basal segment of each chelicera (Fig. 2p).

Paint was applied to each lure shortly after mounting, but before the lure was sprayed with plastic lacquer. The red paint was readily seen by human observers, but salticid photoreceptors are decidedly inefficent at detecting long-wavelength light (i.e., red), being unable to discriminate wavelengths in the red region from green (Blest et al., 1981). For P. fimbriata red paint would probably appear to be simply an exceptionally dark shading.

Results

When data from using an intact salticid lure were compared with data from using the two modified control lures (AM eye centres painted only and AM eye sized circles on chelicerae), there was no significant difference in how often different stalking styles were adopted by P. fimbriata (Table 1). However, there was a significant difference in how often different stalking styles were adopted with the two lures that had the AM eyes completely obscured by paint compared with the intact salticid lure (Fig. 6). Pursuit tendency against any of the modified lures were not significantly different from the pursuit tendency against the intact lure.

Discussion

Cryptic stalking was adopted only when lures included a salticid carapace on which the AM eyes were visible. There was no evidence that removal of palps, legs or the abdomen from a salticid lure influenced P. fimbriatas' tendency to adopt cryptic stalking. Even replacing the

appendages, abdomen and body with that of another animal (i.e., lycosid or house fly) had no apparent influence on P. fimbriatas' tendency to adopt cryptic stalking as long as the salticid carapace was left intact and the AM eyes were still visible.

The AM eyes seem to provide vital cues, and helps explain two findings of our previous study (Harland and Jackson, in prep.). Firstly, the wide range of salticids against which the Queensland Portia adopted cryptic stalking can be explained because the AM eyes are similar in configuration and appearance across almost all salticid species (Coddington and Levi, 1991). Secondly, salticids from the subfamily Lyssomaninae elicited some unusual responses. Lyssomanines tend to be leaf dwellers, with females, but not the males, being unusually translucent. An artifact of translucent cuticle is that, when viewed head on, the AM eyes of lyssomanine females, but not those of lyssomanine males, have light and dark regions that flicker in and out of view. P. fimbriata sometimes adopted ordinary stalking against the females, but never against the males, of all lyssomanine species tested, suggesting that the flickering AM eyes impaired P. fimbriata's ability to identify lyssomanine females.

We investigated the cues used by Queensland P. fimbriata to identify other salticids in the context of predatory versatility (i.e., cues for distinguishing salticids from other categories of prey), but earlier studies on prey-recognition cues used by salticids (Homann, 1928; Heil, 1936; Crane, 1949; Drees, 1952) envisaged salticids facing a simpler problem. In Drees' (1952) study, arguably the most influential, lures (2D drawings and 3D models made of plasticene and wire) were presented to males of Salticus scenicus, establishing that leg characteristics (angle to vertical, thickness, and positioning around the body) were critical. Drees (1952) envisaged his experiments as asking S. scenicus simply to distinguish between two mutually exclusive categories, prey (i.e., insects) and conspecifics (i.e.,salticids). When S. scenicus attacked a lure, this was taken as evidence that the object had been identified as

prey. When S. scenicus displayed, this was taken as evidence that the object had been identified as another salticid. The impression from Drees' study is that S. scenicus relies on leg characteristics alone (especially thickness, density and a particular angle to vertical, 25°-30°) when identifying salticids, with just about any other object of appropriate size being, by default, accepted as prey. Land (1972) concisely summed up the bones of Drees' theory. The perceptual decision process used when a salticid identifies an object can be described by an algorithm: "if it moves, find out whether it has legs in the right places; if it does, mate or avoid it; if it doesn't, catch it."

Drees' algorithm is simple. There are only two discrete classes of object (prey and conspecifics) and they are exclusive in terms of both the cues they provide and the response they require. However, the prevalence of predatory versatility in the Salticidae (Jackson, 1992) was not appreciated in Drees' time. That is, in addition to distinguishing between prey and conspecifics, salticids with pronounced predatory versatility can also discriminate between different types of prey (e.g., flies, worker ants, caterpillars and spiders), and deploy appropriate tactics against each (Edwards et al., 1975; Cutler, 1980; Jackson and Blest, 1982; Freed, 1984; Jackson and van Olphen, 1991).

We might attempt to accommodate predatory versatility in to Drees' algorithm simply by including a new clause for each type of prey. For the Queensland P. fimbriata we might try an algorithm that reads: "find out if the object has large AM eyes; if it does, stalk it using cryptic stalking; if it doesn't, stalk it using ordinary stalking". This algorithm, however, is not adequate for P. fimbriata because the features that provide cryptic-stalking cues (AM eyes) are present not only on salticid prey but also on conspecifics.

Some features of the legs of P. fimbriata's prey provide cues that strongly influence stalking tendency. Removing the first pair of legs and removing more than one pair of legs

reduced stalking tendency. It is tempting to suggest an algorithm for P. fimbriata phrased in the style of Drees: "if the object has enough legs in the right places, then it is prey; if it is prey, determine whether it also has AM eyes; if it does, adopt cryptic stalking; if it doesn't, adopt ordinary stalking". However, even this is an oversimplification because P. fimbriata sometimes stalked salticid lures that had all legs removed. Evidently the cephalothorax (including AM eyes) and the abdomen also influence stalking tendency, but less strongly than cues from salticid legs.

Expressing algorithms in terms of a series of "if" statements joined together to form simple discrete decision trees appears to be inadequate for P. fimbriata. A more appropriate way of expressing an algorithm for P. fimbriata might be to base it on the interactions between a set of independent perceptive processes, each having the task of identifying a specific cue, and a set of response processes, each mediating different predatory tactics. When a perceptive process detects a relevant cue, it might activate one or more response processes. For stalking lures there would be only two relevant response processes: 1) a general predatory response (i.e., to stalk or not to stalk) when activated by some combination of perceptive processes that identify leg-based cues, AM eye-based cues and abdomen-based cues; 2) a more specific predatory response process (i.e., to adopt or not to adopt elements of cryptic stalking: called 'crypsis response' for short) activated only by perceptive processes that identify AM eye-based cues. Expressing the algorithm in this way, what P. fimbriata does when confronted with a lure (i.e., what we observe) depends on whether one, the other or both response processes have been activated (Fig. 7). When the crypsis response is activated, but the general predatory response process is not, no stalking at all is triggered. When the general predatory response process is activated, but the crypsis response process is not, stalking is triggered, but with the style being ordinary stalking. When both the general

predatory response process and the crypsis response process are activated, cryptic stalking is observed.

Each response process might be influenced to different degrees by different cue-identification processes. This might be seen as a probability of a perception process, once activated, activating, in turn, a response process. The crypsis response process would be influenced strongly by the perceptive process that identifies the AM eye-based cues, whereas the general predatory response process might be influenced strongly by the perception process that identifies leg-based cues, but only weakly by the perception process that identifies abdomen-based cues and the process that identifies AM eye-based cues.

Acknowledgments

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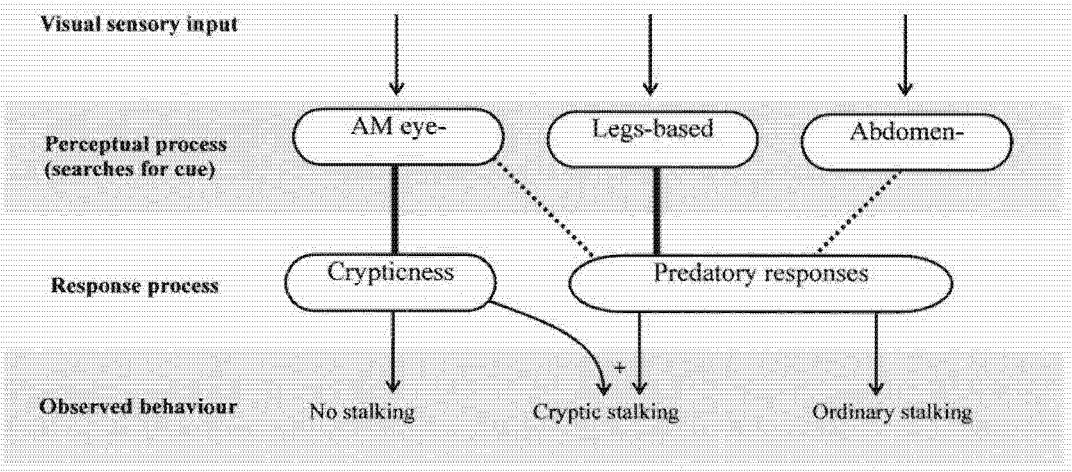

Fig. 7. Proposed decision structure for the Queensland Portia fimbriata when confronting a lure. Perceptual processes search visual input for specific cues. When these cues are found, perceptual processes may activate response processes. Combination of activated response processes determines observed behaviour. Perceptual processes can have either a strong (solid lines) or a weak (dashed lines) influence on response processes.

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Table 1. Predation data for *P. fimbriata* and intact and modified lures.

Lure	N	Stalking tendency[1]	Cryptic stalking[2]	Ambivalent stalking[2]	Ordinary stalking[2]
Intact salticid	224	83%	82%	14%	4%
Intact lycosid	70	73%	0%	16%	84%
Intact house fly	152	43%	0%	0%	100%
Salticid, both palps removed	50	78%	97%	3%	0%
Salticid, one leg I removed	49	71%	89%	11%	0%
Salticid, both legs I removed	81	67%	85%	11%	4%
Salticid, legs I and II removed	74	61%	78%	18%	4%
Salticid, both legs II removed	51	80%	95%	5%	0%
Salticid, legs I, legs II, and both palps removed	96	54%	79%	19%	2%
Salticid, all legs removed	131	40%	73%	21%	6%
Salticid, all legs and both palps removed	122	46%	63%	27%	11%
Salticid, all legs, both palps, and abdomen removed	179	27%	67%	27%	6%
Salticid, AM eyes painted over (outlines obliterated)	59	69%	0%	12%	88%
Salticid, AM eye painted over (outlines obliterated) and both palps removed	69	61%	0%	10%	90%
Salticid, centres of AM eyes painted over (outlines intact)	28	75%	57%	33%	10%
Salticid, paint on chelicerae and both palps removed	59	69%	90%	10%	0%
Lycosid with salticid carapace atop its own carapace	63	78%	92%	6%	2%
Fly with salticid carapace placed on head and thorax	59	54%	63%	31%	6%

1. Percentage of N

2. Percentage of total number stalking (i.e., cryptic stalking, ambivalent stalking and ordinary stalking sum to 100%)

Chapter 7. Features of the anterio-median eyes of salticids that provide prey-specific cues to *Portia fimbriata*

Introduction

Portia fimbriata adopts cryptic stalking against a varied range of salticids (Chapter 5). Lures with features altered suggest the cues that allow *P. fimbriata* to discriminate salticids from other kinds of prey (Chapter 6). The carapace alone to triggers *P. fimbriata*'s salticid-specific predatory tactics (cryptic stalking), but only if the large principal, or anterio-median (AM), eyes are visible on the carapace. A tentative conclusion from these studies is that the AM eyes of salticids provide the most critical cues that trigger cryptic stalking cryptic stalking (Chapter 5 & 6). Here the aim is to investigate in greater detail the features of the AM eyes that are effective as cues. This is a step toward a long-term goal of clarifying the perceptual processes governing salticid predatory behaviour.

In the previous study (Chapter 6), entire body parts or appendages were removed from lures. The influence of more fine-grain features of salticid appearance are investigated here. To a person the AM eye of a salticid have the appearance of a pair of dark glossy hemispheres protruding from the anterior surface of the carapace, one on either side of the sagittal plane of the body. Altering fine details of the principal eyes while controlling for other potential influences from *P. fimbriata*'s response would be exceedingly difficult, if not impossible. As an alternative, computer-generated virtual lures were used. As a standard, virtual lure depicting *Jacksonoides queenslandicus* female was used. Experimental lures were made by systematically altering the appearance of the standard lure. Specific abstracted features of the AM eyes were investigated.

Materials and methods

Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier spider studies (Jackson and Hallas, 1986). Testing was carried out between 0900 h and 1700 h (laboratory photoperiod 12L:12D, lights on at 0800).

Individuals of *P. fimbriata* were chosen at random from the stock culture for each specific test. Each individual *P. fimbriata* tested was reared from an egg in the laboratory. Hunger state was standardized before testing by keeping each individual without prey for 5 days.

Lures were presented to *P. fimbriata* using the Virtual Lure Presentation System (VLPS), described in Chapter 3. The testing arena for these experiments was a platform (80 mm long x 65 mm wide) placed in front of, and level with the bottom of, a projector screen (behind two glass filters), and 160 mm above the table surface (Fig. 1). The platform consisted of a wire frame (brass welding wire, diamter 1.5 mm) over which was stretched multiple layers of non-sticky (structural) silk threads from *Badumna longinquus* (Desidae), a web-building spider. Silk threads were stretched over the frame in quantities sufficient to make a dense matting with no large holes large enough for *P. fimbriata* to pass. As a precaution against possible chemical traces left by previously tested *P. fimbriata*, the web platform was washed in a bath of 80% ethanol, then allowed to dry for at least 30 min, between tests.

Lighting was from fluorescent tube ceiling lights 1.5 m above the platform (approx. 675 lux at platform surface). The projector screen by itself provided some additional light (~85 lux at 10 mm from screen).

Before each test, a *P. fimbriata* was transferred from its cage to a small plastic petri dish using a small soft-tipped paintbrush to direct its movements. From the petri dish, *P. fimbriata* was introduced into a narrow opaque tube (internal diameter 13 mm, length 45 mm)

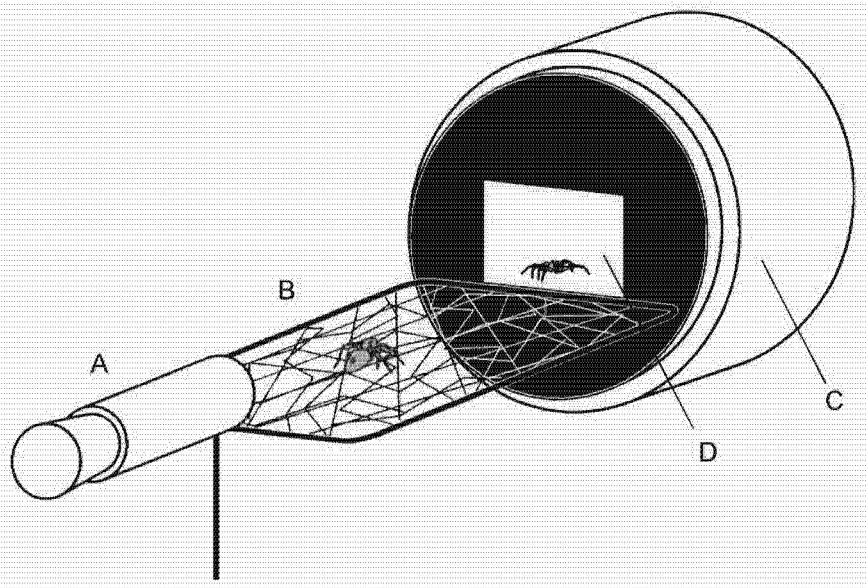

Fig. 1. Set up for presenting virtual lures to *Portia fimbriata*. (A) Opaque tube, stoppered at one end. *P. fimbriata* emerges from non-stoppered end, fringed with hair (not shown). (B) Web platform, wire frame matted with silk. (C) Lens array for reducing image from computer projector (not shown) to life-like size. (D) Image from lens array: virtual salticid lure on uniform white background.

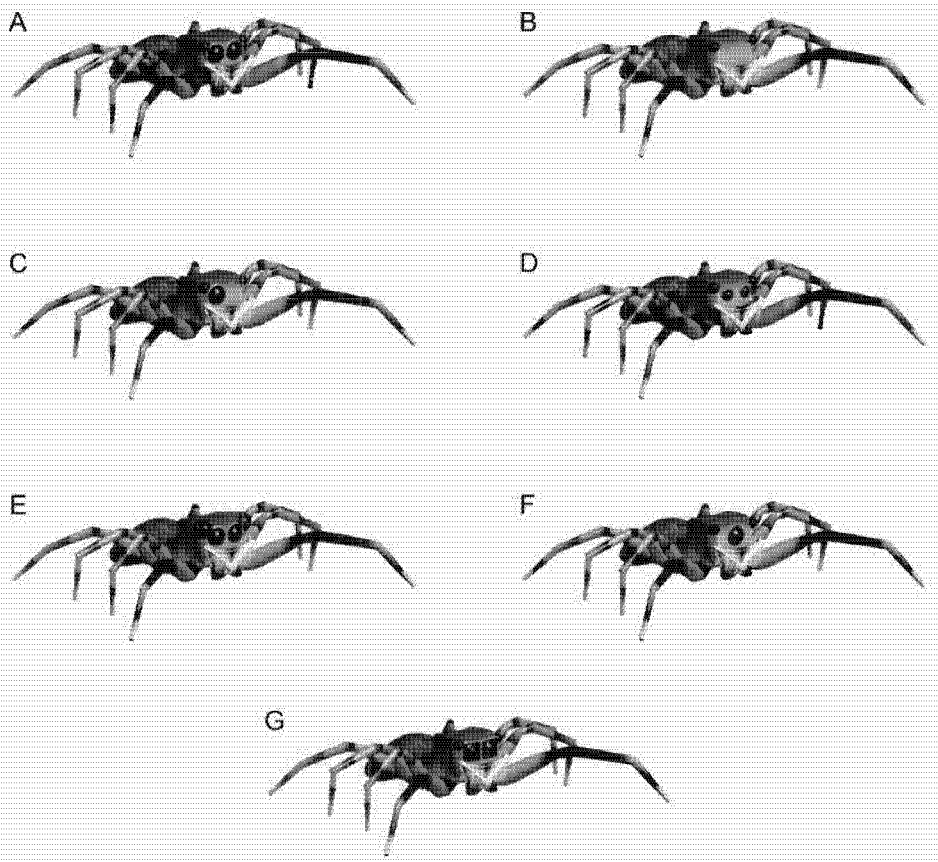

Fig. 2. Virtual lures based on *Jacksonoides queenslandicus* females; (A) intact, (B) with no anterio-median (AM) eyes, (C) with one AM eye, (D) with AM eyes reduced to size of anterior-lateral (AL) eyes, (E) with AL eyes increased to size of AM eyes, (F) with one AM eye centred on face, (G) with square AM eyes.

attached to the wire frame opposite the screen. The tube faced the projector screen. One end of the tube touched the web and the top and sides of this end were fringed with human hair to discourage *P. fimbriata* from climbing on top of the tube (~7.5 mm long and held in place with tape). *P. fimbriata* was introduced into the end of the tube that was away from the screen and this end was then stoppered to ensure that *P. fimbriata* could only exit from the end of the tube towards the screen. Before a test could begin, *P. fimbriata* had to emerge from the tube onto the web and had to begin stalking the lure. After 15 min had elapsed, if *P. fimbriata* still had not left the tube a small soft-tipped brush was used to direct it gently until it was facing the screen, after which it was allowed an additional 15 min to emerge. If it still did not emerge, the test was abandoned.

Virtual lures were presented on a white screen (23.5 mm wide x 17.5 mm high) using only shades of grey. The zoom level of the projected image was finely tuned so that the standard intact *J. queenslandicus* lure was the same size as a real mature female *J. queenslandicus* (carapace width to nearest 0.1 mm). Each virtual lure could be moved horizontally and vertically across the screen, and could be made to rotate smoothly around its vertical axis.

Before *P. fimbriata* left the tube, the lure was moved erratically back and forth on the screen. Once *P. fimbriata* walked out of the tube and onto the platform the erratic movement of the lure was continued until *P. fimbriata* oriented toward the lure. After which the lure was halted and then moved to the centre of the screen. Tests began only when *P. fimbriata* began stalking the lure. Because the objective of the study was to look at the different stalking styles elicited by lures, sequences in which *P. fimbriata* did not stalk the lure were ignored.

Once stalking began, the lure was rotated ~45°, at random to the left or right. For *P. fimbriata*, palp positioning (whether in front of or beside the chelicerae) and walking style (whether smooth or choppy) were recorded. Two specific tests were carried out next. To

ensure that *P. fimbriata* was actually stalking the lure, rather than just walking toward the part of the screen where the lure was situated, the lure was moved 10 mm to the left or the right. If *P. fimbriata* changed its course to follow the lure, it was considered to be stalking the lure and the test continued. If *P. fimbriata* did not follow the lure, the test was aborted.

When *P. fimbriata* had stalked to within 50 mm of the lure, a second test was carried out to determine if *P. fimbriata* would freeze when suddenly faced by the lure. The lure (initially facing 45° to the side) was instantly (i.e., without any in-between steps) made to face towards *P. fimbriata*. Whether *P. fimbriata* froze (i.e., stopped all movement) within ~0.5 sec of being faced, was noted. The 'freezing test' was carried out two more times. *P. fimbriata* will sometimes freeze when stalking a prey that has just stopped moving (Wilcox et. al 1996). To distinguish between 'freezing when prey halts' and 'freezing when faced', the lure was halted for ~2 sec after being rotated 45° left or right but before being made to instantly face *P. fimbriata*. If *P. fimbriata* froze when the lure stopped during the halted period, the lure was kept stationary until stalking began again. I ended tests either when the three freezing tests had been completed or if *P. fimbriata* touched the glass after only two freezing tests had been completed.

Two categories of stalking were recognized, cryptic stalking (choppy walking style, consistent adoption of the retracted-palps posture and freezing at least 2 x when faced by the lure) and ordinary stalking (consistent adoption of the same posture used during ordinary locomotion, including the holding of palps loosely in front of the chelicerae, and failure to freeze in more than 1 freeze tests).

Paired testing was implemented, each individual *P. fimbriata* being tested once with an intact lure and once with a modified lure. Testing order (i.e., intact lure then modified lure or modified lure then intact lure) was chosen at random. *P. fimbriata* was returned to the

small plastic petri dish and placed out of sight of the testing apparatus during the interval (10-15 min) between the first and second test. Paired frequency data for stalking style and tendency to freeze were analysed using the chi-square McNemar test for significance of changes.

Using the methods described in Chapter 3, a total of seven virtual lures were made (Fig. 2). An intact lure (Fig. 2a) was based on a *J. queenslandicus* female. Experimental lures (Fig. 2b-g) were based on modifying a copy of the intact lure.

Table 1. Summary data from paired tests of *Portia fimbriata* with an intact lure and a modified lure.

Modified lure	N	Froze when faced by modified lure	Froze when faced by intact lure	Cryptic stalking with modified lure	Cryptic stalking with intact lure
No AM eyes	14	14%	79%	0%	64%
One AM eye (normal position)	12	67%	92%	67%	67%
Small AM eyes	12	8%	83%	0%	67%
Large AL eyes	12	75%	58%	58%	58%
One AM eye (centred)	12	17%	83%	8%	42%
Square AM eyes	13	23%	100%	15%	85%

Influence of the number of AM eyes

Methods

Two lures (Fig. 2b, c) were made. A lure with both AM eyes removed (Fig. 2b) replicated previous work using physical lures (Chapter 6), thereby providing a control for possible confounding effects of using the VLPS. The lure with only one AM eye (Fig. 2c) was made by removing the left AM eye from a copy of the intact lure.

Results

Individual *P. fimbriata* more often ($P<0.01$) adopted cryptic stalking against, and more often froze when faced by ($P<0.01$), the intact lure compared with the lure that had both AM eyes removed (Fig. 3a), with cryptic stalking never being adopted against the lure with no AM eyes (Table 1 & 2). However, no evidence was found of individuals adopting cryptic stalking, or freezing when faced, more often or less often with the intact lure compared with the lure with one AM eye.

Influence of the size of AM eyes

Methods

Two lures (Fig. 2d, e) were made. One had AM eyes with their diameters reduced to that of the anterio-lateral (AL) eyes (Fig. 2d). The other, AL eyes enlarged to the diameter of AM eyes (Fig. 2e). For both lures, the position of the centre point of each AM and AL eye was preserved.

Results

Individual *P. fimbriata* more often ($P<0.01$) adopted cryptic stalking against, and more often froze when faced by ($P<0.01$), the intact lure compared with the lure with small AM eyes (Fig. 3b), with cryptic stalking never being adopted against the lure that had small AM eyes (Table 1 & 2). However, no evidence was found of individuals adopting cryptic stalking, or freezing when faced, more often or less often against the intact lure compared with the lure with enlarged AL eyes.

Influence of the position of AM eyes

Methods

A lure was made with one AM eye removed, the remaining eye repositioned horizontally so that it was in the centre of the spider's 'face' (Fig. 2f).

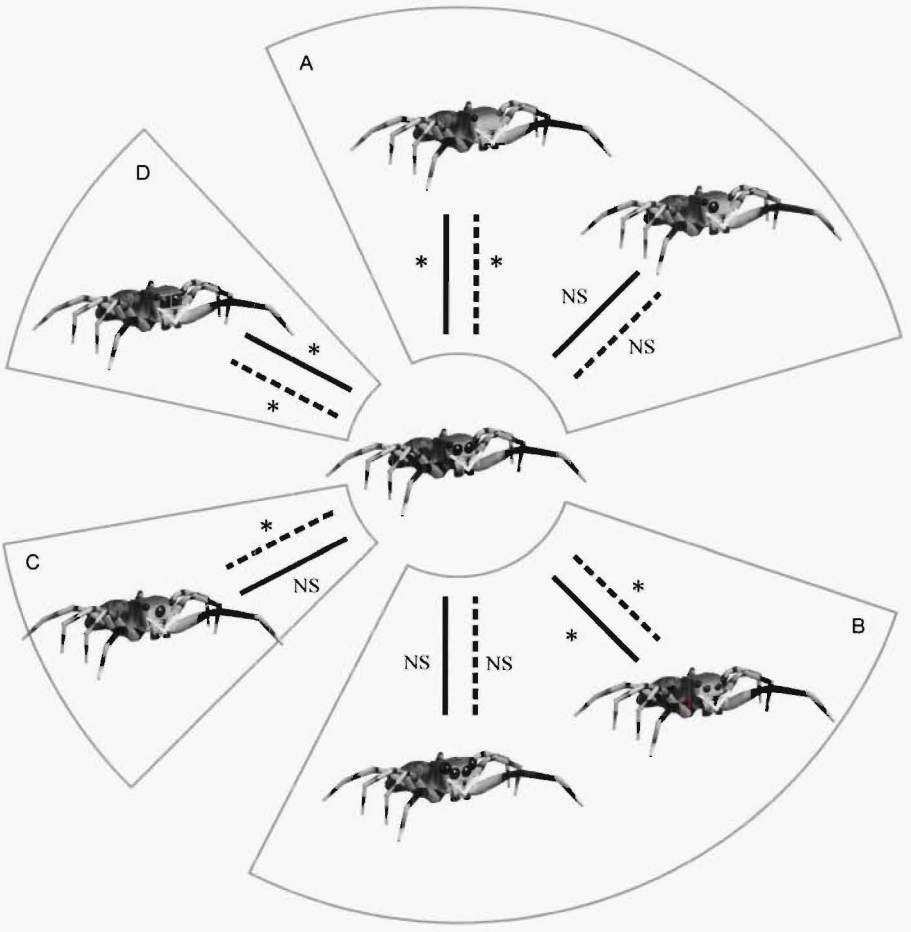

Fig. 3. Results from paired tests. Each time, intact salticid lure (centre) and one modified lure compared. Comparisons of tendency of individuals to adopt cryptic stalking (solid line) and freeze when faced by lure (broken line). (A) Modified lures used to test effect of number of AM eyes. (B) Modified lures used to test effect of anterio-median (AM) eye size. (C) Lure used to test effect of AM eye position. (D) Lure used to test effect of AM eye shape.

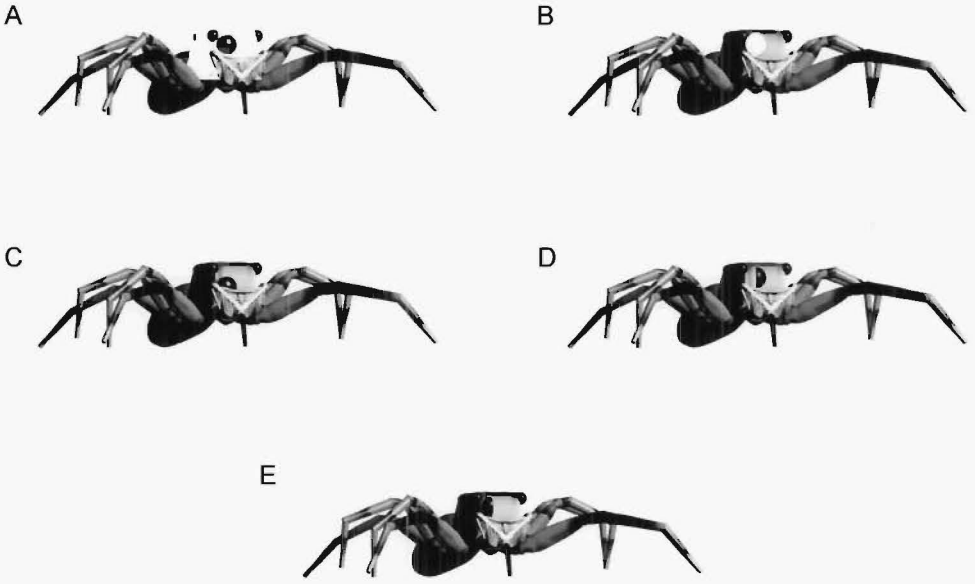

Fig. 4. Proposed virtual salticid lures for future tests that lead on from current study. (A) Lure with one anterio-median (AM) eye removed and white (cryptic but opaque) carapace. (B) Lure with one AM eye removed and the other white. (C) Lure with one AM eye removed and the other repositioned vertically. (D) Lure with one AM eye removed and the other with its lateral half removed. (E) Lure with one AM eye removed and the other with its medial half removed.

Results

No statistical evidence was found to suggest that how often individual *P. fimbriata* adopted cryptic stalking was influenced by whether lure had one centred AM eye or was the intact lure. However, individual *P. fimbriata* more often ($P<0.01$) froze when faced by the intact lure than when faced by the modified lure (Fig. 3c) (Table 2).

Influence of the shape of AM eyes

Methods

A lure was made with both AM eyes replaced with square eyes, each having an edge length the same as the normal AM eye's diameter (Fig. 2g). The central region of each square AM eye was made to bulge out the same distance as the normal AM eye, thereby preserving the shape of the eye when viewed from the side and preserving the specular.

Results

Individual *P. fimbriata* more often ($P<0.01$) adopted cryptic stalking against, and more often froze when faced by ($P<0.01$), the intact lure compared with the lure with square AM eyes (Fig. 3d) (Table 1 & 2).

Table 2. Results from McNemar tests comparing the frequency with which individual *P. fimbriata* adopted different tactics with the intact lure and modified lures.

Modified lure	Freeze when faced	Choppy walk	Retracted palps	Cryptic stalk
No AM eyes	$P<0.01$	$P<0.05$	$P<0.01$	$P<0.01$
One AM eye (normal position)	NS	NS	NS	NS
Small AM eyes	$P<0.01$	$P<0.05$	NS	$P<0.01$
Large AL eyes	NS	NS	NS	NS
One AM eye (centred)	$P<0.01$	NS	NS	NS
Square AM eyes	$P<0.01$	$P<0.05$	$P<0.05$	$P<0.01$

Discussion

The cues used by the Queensland *P. fimbriata* to discriminate between salticid and non-salticid prey were investigated by means of modifying specific abstracted features of the AM eyes (i.e., number, size, position and shape). Some features had no apparent effect on *P. fimbriata*'s ability to make this discrimination and most likely play no part in the perceptual process. The remaining features can be discussed in terms of the perceptual process.

Results from tests using the lure with no AM eyes are consistent with findings from Chapter 6, suggesting that that the AM eyes are features of the Queensland *P. fimbriata*'s salticid prey that provide cues critical for eliciting cryptic stalking. However, this conclusion can not be this simple because results from the lure with one AM eye removed and the other AM eye in its normal position, imply that only one AM eye is necessary.

Results from testing with the lure that had AM eyes reduced in size imply that AM eyes must be large to act as a cue. Increasing the size of the AL eyes does not appear to have an effect. Nor does a single AM eye's horizontal position have a apparent role as a cue for cryptic stalking, but it does affect *P. fimbriata*'s tendency to freeze when faced by salticid prey. When the lure had square edged AM eyes, it was not treated as salticid prey, implying that the shape of the edges of the AM eyes is important because.

In short, the perceptual process used by *P. fimbriata* to identify salticid prey apparently requires the presence of at least one AM eye that is large enough and has curved edges. Adjusting these features of the AM eye affects *P. fimbriata*'s tendency to retract its palps, walk in a choppy manner and freeze when faced by the prey salticid. However, more information about the abstracted feature of AM eye size and shape is required before we can formulate a specific hypothetical process.

When determining the size of a spider's AM eye, *P. fimbriata* must compare it to some other feature of the salticid. Relying on absolute eye size is not an option because absolute eye size varies with the size prey salticids and their distance from *P. fimbriata*. That the process used to determine AM eye size is based on comparing the relative size of the AM and AL eyes can be ruled out because the lure with reduced AM eyes was treated differently from the intact lure whereas the lure with enlarged AL eyes was not.

Another potentially confounding factor when investigating the effects of AM eye size is that reducing or enlarging only the AM eyes always changes the position of some parts of the eye relative to some parts of the carapace. For example, when reducing the size of AM eyes on lures, the position of the centre of each AM eye was preserved (i.e., kept the same as on the intact lure), but this meant that the edges of the reduced AM eyes had changed position relative to other features of the carapace (e.g., AL eyes and edge of carapace). Distance between the edge of the AM eye and another feature of the salticid face could be used as a basis of comparison when determining eye size (e.g., distance between edge of AM and edge of AL eye or distance between edge of AM eye and edge of carapace). Some of these possibilities can be ruled out by examining results from tests that used the lure with a single horizontally centred AM eye. By horizontally centring the AM eye on the face, the horizontal component of distances between the edge of the AM eye and other facial features (e.g., AL eyes and lateral edge of carapace) were greater than for the lure which had AM eyes that were reduced in size. *P. fimbriata* tended to adopt cryptic stalking against the lure with reduced AM eyes, but not against the lure with one horizontally centred AM eye. This suggests that the horizontal component of distances between the edge of the AM eye and other facial features is not used to determine AM eye size.

The objective in this initial series of experimental lures was to narrow down, from a wide range of hypothesis about feasible features, a small set of features of the AM eyes about which more specific questions could be asked. More lures can now be designed to further clarify the size and shape related features of the AM eye that serve as critical cues. A second series of five lures is suggested (Fig. 4).

- A lure that has a white (i.e., invisible but opaque) carapace and one AM eye (Fig. 4a) This would be a way of testing the hypothesis that eye size is based on comparing AM eyes with some other feature of carapace.

- A lure that has a single AM eye of normal size, shape and position, but with a white centre (Fig. 4b).

- A lure that has one AM eye with normal horizontal position, but positioned lower than usual on the face (Fig. 4c). This would be a way of testing whether the vertical distance between edge of AM eye and top of carapace is used to determine AM eye size.

- A lure that has one AM eye cut in half and with squared medial edges and rounded lateral edges (Fig. 4d). This would be a way to test whether medial edges alone provide critical shape cues.

- A lure that has one AM eye cut in half and with rounded lateral edges and squared medial edges (Fig. 4e). This would be a way to test whether lateral edges alone provide critical shape cues.

In addition to clarifying the specific AM-eye features that sever as cryptic-stalking cues, results from the present study have revealed some details of a second process at work within the context of cryptic stalking. Although there was no evidence that the tendency to adopt cryptic stalking was affected by adjusting the horizontal position of a single AM eye, the tendency to freeze when faced by the lure was affected. Individual *P. fimbriata* less frequently froze when faced (Table 2) with the lure with one horizontally centred AM eye compared to the intact lure. This suggests that freezing when faced and other parts of the cryptic stalking response may be triggered by different cues.

Freezing when faced differs from the other components of cryptic stalking because, unlike retracted palps and choppy walking, freezing when faced is expressed not simply when the prey is a salticid, but specificially when the prey is a salticid that is behaving in a specific way (i.e., facing *P. fimbriata*). When *P. fimbriata* sees a prey with an AM eye, it will adopt the choppy walking and retract its palps, but will not freeze except when the prey faces directly towards *P. fimbriata*. We cannot rule out that freezing when faced is primed by the same cues that trigger the other components of the cryptic stalking response, but the cues that trigger its expression are probably different.

It is now possible to isolate two different, but related, questions for further investigation. The original question (how does *P. fimbriata* know that a spider is a salticid?) is joined by a new question: "given that *P. fimbriata* knows the spider is a salticid, how does it know when it is being directly faced by the salticid?" Presumably the features of salticid prey that provide the cues that answer these two questions are similar (i.e., size and shape of the AM eye is important), but not exactly the same (i.e., horizontal position of AM eye is important only for freezing when faced).

From *P. fimbriata*'s perspective, we could say that deciding whether you are being faced by a salticid is a more difficult task than simply looking to see if the AM eyes are visible (or even, one AM eye is visible). This is because the AM eyes are visible from a wide range of angles. For example, they are still easily seen when the salticid is facing 45° to the left or the right (Fig. 2), and when the salticid is oriented at this angle *P. fimbriata* does not freeze (Chapter 6). The results from testing with the lure with one horizontally centred eye suggests that the horizontal distance between the edge of the AM eye and the visible edge of the carapace provides a the cue that tells *P. fimbriata* when to freeze. As the intact prey salticid turns from a facing position, the distance between the edge of the widdershins AM eye (i.e., the one in the opposite direction to the turn's direction) and the visible edge of the carapace increases very rapidly as more of the side of the carapace comes into view (Fig. 5).

P. fimbriata might measure this distance by first fixing its AM retina on the pattern made by the curved edge of the lure's widdershins AM eye and then moving its retina horizontally (thereby, moving its viewpoint over the image of the salticid) until the edge of the carapace is observed. Comparing this measurement with either the distance of the spider from *P. fimbriata* (i.e., its range) or its size (i.e., size as established by other cues) would give an accurate measure of how closely the salticid is facing *P. fimbriata.* Further evidence for testing this hypothetical process might be gained from testing using the lures previously proposed (Fig. 4).

If this hypothetical perceptual process is supported by further evidence it might explain one of the unusual finding from Chapter 5. *Pachyballus cardiforme* is, at least to the human eye, an especially convincing beetle mimic (Fig. 6). Almost half of the *P. fimbriata* tested with *P. cardiforme* classified it as prey (i.e., they stalked it), but only one (of 7 that stalked) adopted cryptic stalking. The remaining *P. fimbriata* that stalked *P. cardiforme,*

Fig. 5. Rapid increase in distance between edge of anterio-median (AM) eye and edge of visible carapace (red line) during a turn. (A) lure facing at 0°, 30° and 45° from front. Note how this distance increases much more rapidly than each AM eye's edge-to-edge distance decreases with increasing angle.

Fig. 6. *Pachyballus cardiforme*. A beetle-mimicking salticid. Front view. Note the relatively wide distance between the lateral edges of the anterio-median eyes and the lateral edges of the carapace.

adopted ambivalent stalking and did not consistently freeze when faced. Possibly as a consequence of its resemblance to beetles, *P. cardiforme*'s AM eyes are horizontally centred on a wide face. The distance between the lateral edges of *P. cardiforme*'s AM eyes and the edges of the carapace is, compared with other salticids, relatively large even when facing; potentially affecting *P. fimbriata*'s perceptual process.

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Chapter 8. A knife in the back: discrimination of prey orientation and target choice by *Portia*

Introduction

How *Portia* uses vision to discriminate between different prey types (e.g.,, salticid spider versus non-salticid spider) was considered in Chapters 6 & 7. Adoption of prey-specific predatory tactics served as evidence of perception. In Chapter 7, two separate levels of control and visual discrimination were discussed in relation to salticid-specific responses. The AM eyes of salticid prey are critical cues. Perceiving these cues influences *P. fimbriata*'s immediate behaviour (adopting choppy walking while holding palps retracted) and also primes *P. fimbriata* to freeze when the salticid prey is facing. An implication of these findings is that when *P. fimbriata* identifies a prey as a salticid, this not only just triggers an immediate response but also influences a more general set of perceptual and decision-making processes.

Freezing when faced is an important part of cryptic stalking, but it entails more than simply identifying prey as being a salticid. *P. fimbriata* must identify the prey's orientation. When the prey is a salticid, *P. fimbriata* can rely on cues that are unique to salticid prey (i.e., the large AM eyes). Large AM eyes directed towards *P. fimbriata* can serve as a cue for this type of prey orientation.

In this chapter, the importance of orientation is investigated when the prey is not a salticid. Preliminary studies suggest that all species of *Portia*, including *P. fimbriata*, often attack a variety of spiders other than salticids from directly behind. *Badumna* spp., for example, are common prey of *P. fimbriata* in nature and attacks on these exceptionally powerful spiders appear to be, from casual observation, especially often from the rear. However, attacking from the rear does not appear to be a rule applied by *Portia*

indiscriminately to all prey. Pholcids appear to be especially pronounced exceptions. These are spiders with extremely long legs, and preliminary observations suggest that *Portia*'s objective when orienting attacks is primarily to avoid hitting one of a pholcid's legs (see Jackson & Wilcox 1998). Whether or not a pholcid is facing away appears to be more or less irrelevant.

The present chapter is an experimental study of whether *Portia* makes different decisions when orienting attacks depending on whether the prey is *Badumna longinquus* or *Pholcus phalangioides*.

Materials and Methods

Study animals

Three species of *Portia* were used, *P. fimbriata* (Doleschall) (Queensland, Australia), *P. labiata* (Thorell) (Luzon, Philippines) and *P. africana* (Simon) (Uganda). The prey, *Badumna longinquus* (L. Koch) (Desidae) and *Pholcus phalangioides* (Fuesslin) (Pholcidae), are web-building spiders. *B. longinquus*, a stocky spider with thick legs and powerful chelicerae, attacks prey and potential predators by lunging forwards to bite. *P. phalangioides* uses its long thin legs for rapidly wrapping up prey with silk from a distance. Despite having only small, weak chelicerae, *P. phalangioides* is a formidable predator. House flies, *Musca domestica* L. (body length ~6 mm), and fruit flies, *Drosophila immigrans* (Sturtevant) (body length ~4 mm), were also used as prey. *Portia* used in this study came from laboratory cultures and were all adult females or large juveniles. House flies and fruit flies also came from cultures. *B. longinquus* and *P. phalangioides*, being common introduced species in New Zealand, were collected locally.

Maintenance and General Procedures

Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier spider studies (Jackson & Hallas 1986). All testing was carried out between 0830 h and 1730 h (laboratory photo-period 12L:12D, lights on at 0800). No individual *Portia* was used in more than one test.

Each *Portia* was maintained without feeding for 7 to 10 days prior to being tested. For each test, a prey was chosen (either a spider or an insect). Estimated body length of the prey was always 75-100% that of the *Portia* with which it was tested. Tests were executed in transparent plastic cages (diameter 90 mm, height 125 mm).

A number of factors complicate interpreting findings from experiments where natural webs are used. The webs of *B. longinquus* and *P. phalangioides* are complex three dimensional structures where it is difficult to determine precisely the relative orientation of prey and predator without changing viewing angle and potentially disturbing the predator or prey. What is more, there is considerable web-to-web variation in structure, with the internal structure of any given web varying as well. This means that the position of *Portia* relative to the prey spider within a web may limit the range of possibilities when *Portia* is lining up an attack.

Rather than use natural webs, I used reduced webs where predatory sequences could be observed under more uniform conditions, with *Portia* having few restrictions on its range of possible attack directions. This was achieved by first allowing *Portia* a week to construct a thick web that more-or-less filled the cage to be used as a test chamber. Immediately before a test began, *Portia* was transferred into a small petri dish and most of the web in the cage was removed, leaving only silk lines that ran along (i.e., were within c. 2 mm of) the cage surface. This was achieved by using forceps to remove threads a few at a time.

Experimental procedure

Using a small paintbrush, prey spiders were introduced (herded) from a plastic vial (60 mm long; diameter 25 mm) into the web before testing began. Each prey spider was allowed ~ 2 min to wander around and settle down before *Portia* was introduced and observation began. During this 2-min pre-test period, *P. phalangioides* almost always ascended to the top of the cage and laid down a few lines from which to hang upside down. After moving about in the cage, *B. longinquus* eventually settled with its ventral surface against the web or a plastic surface of the cage.

Flies were knocked out using CO_2 gas and then allowed to recover until they could walk, but not yet fly, before being introduced (herded) into webs. They typically walked or flew to the top of the cage where they settled with their ventral surface against the silk or a plastic surface of the cage, or else they became entangled in the silk, in which case the direction in which their ventral surfaces pointed was unpredictable. By the time that *Portia* was introduced (~2 min later), flies had fully recovered from the CO_2.

Once the prey and *Portia* were in the test chamber, the lid was replaced. Observations began when *Portia* first oriented toward the prey and continued until the prey was captured, *Portia* lost interest (definition: turned away from prey and no longer stalked) or *Portia* remained quiescent for 60 min.

The objective was to look specifically at how *Portia* oriented attacks on these three kinds of prey. Sequences in which *Portia* did not attack and then hold on to the prey were ignored. Likewise, sequences in which the prey moved more than one body length in any direction after *Portia* had begun stalking were ignored. This left a highly simplified data set that could be used, with minimal ambiguity, to test the hypothesis that *Portia* adjust attack orientation differently for different kinds of prey.

Terminology

Orientation of *Portia* to the prey is specified by the region of the prey closest to *Portia.* During stalking, *Portia* almost always faced directly toward the prey. Angular fields of approach, called 'sectors', are used for defining the regions of prey. Each sector covered 45° horizontal by 45° vertical (Fig. 1). Although 26 sectors were defined in this way, this number was reduced to 17 by pooling data from regions that were left-right mirror images of each other. For example, should *Portia* attack facing the prey's flank from 30° above the horizontal plane, the attack would be recorded as being from the 'lateral dorsal'sector, ignoring whether it was left or right.

'Stalking' was defined as head-on movement toward prey. 'Attacking' was defined as lunging from close range at the prey. 'Capturing' was defined as gripping and holding onto the prey after an attack. 'Feeding' was defined by when *Portia* began to pump digestive fluids in and out of the prey. The sector of the prey toward which *Portia* faced was noted when *Portia* initiated stalking, at the moment of attack, when *Portia* captured the prey and during feeding. The body part (cephalothorax or abdomen for spiders; head, thorax or abdomen for the flies) that *Portia* gripped when capturing the prey was also recorded.

Data from different species of *Portia* were pooled. Although analysis without pooling would have been preferable, at the time of testing, fluctuating populations of lab-reared *Portia* spp. cultures, rather than preference, dictated my choice of test subject. However, each species of *Portia* tested faces similar types of prey, with similar behaviour and body form, (i.e., long-legged pholcids, stocky and powerful spiders similar to desids and dipterans) in nature, and there were no obvious differences between data for different species. Data were analysed using chi-square tests of independence, with Bonforoni adjustments when necessary.

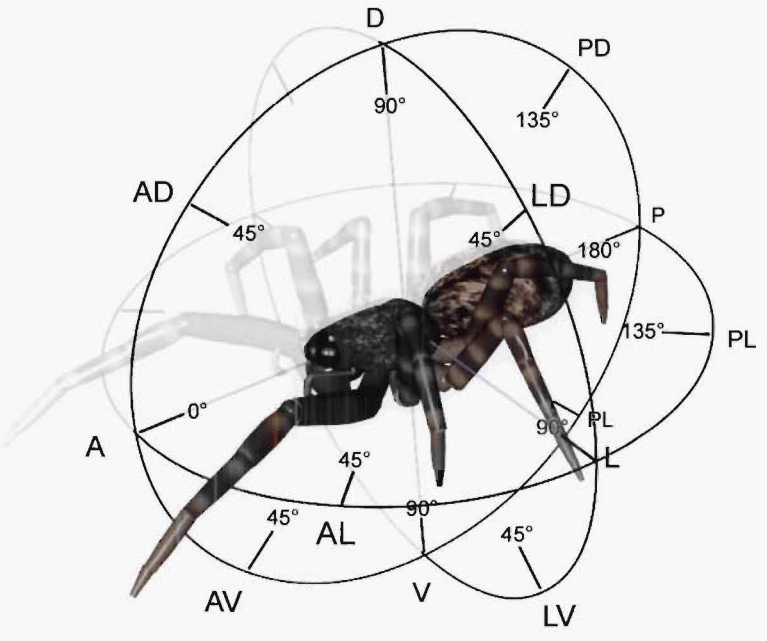

Fig. 1. Sectors, alternative fields of approach towards the prey used to define *Portia*'s orientation to prey. Each sector covers 45° vertical and 45° horizontal. *Badumna longinquus* illustrated here, but same system used for all prey types. A: anterior. D: dorsal. V: ventral. P: posterior. Other sectors labelled as combinations of A, L, V and P. Not depicted, but used, ALD, ALV, PLD and PLV.

Results

Initiation of stalking

Regardless of prey type, *Portia* usually ascended a wall of the cage once a test began, intermittently pausing and scanning the surroundings (for a description of scanning, see Tarsitano & Jackson 1997). It was often during these scanning bouts that *Portia* first oriented toward the prey. Irrespective of whether *Portia* was scanning or not, orientation toward the prey was especially likely if the prey moved.

When stalking began, *Portia*'s orientation was highly variable (Fig. 2). This was because *Portia* typically started stalking immediately after first turning to face the prey, whatever the prey's orientation might be (i.e. whatever sector *Portia* might be in). However, all three types of prey tended to hold their ventral sides toward the cage surface, and this made it unlikely that *Portia* would be in the prey's ventral sector when stalking began. Two of the prey, *B. longinquus* and flies, appeared to attract more or less the same proportion of approaches from sectors along different longitudes (Fig. 2) (e.g., number of approaches from sectors A, AL, L, PL and P were similar, and approaches from sectors AD, ALD, LD, PLD and P were similar). *P. phalangioides* had a longer, thinner body shape (mean carapace width to body length ratio, 1 : 4.5; n = 10) than *B. longinquus* (width to length, 1 : 2.6; n = 10) or flies (width to length, 1 : 2.8; n = 10). This probably accounts for why *Portia* especially often initiated stalking from the lateral sector when the prey was *P. phalangioides*.

Direction of attack on Badumna longinquus

Evidence that *Portia* uses information about *B. longinquus*' orientation to align its attacks from a specific sector comes from comparing differences in the number of *Portia* that approached and the number that attacked from each sector. If *B. longinquus*' orientation had not been important to *Portia*'s strategy (i.e., the null hypothesis), we might have expected that

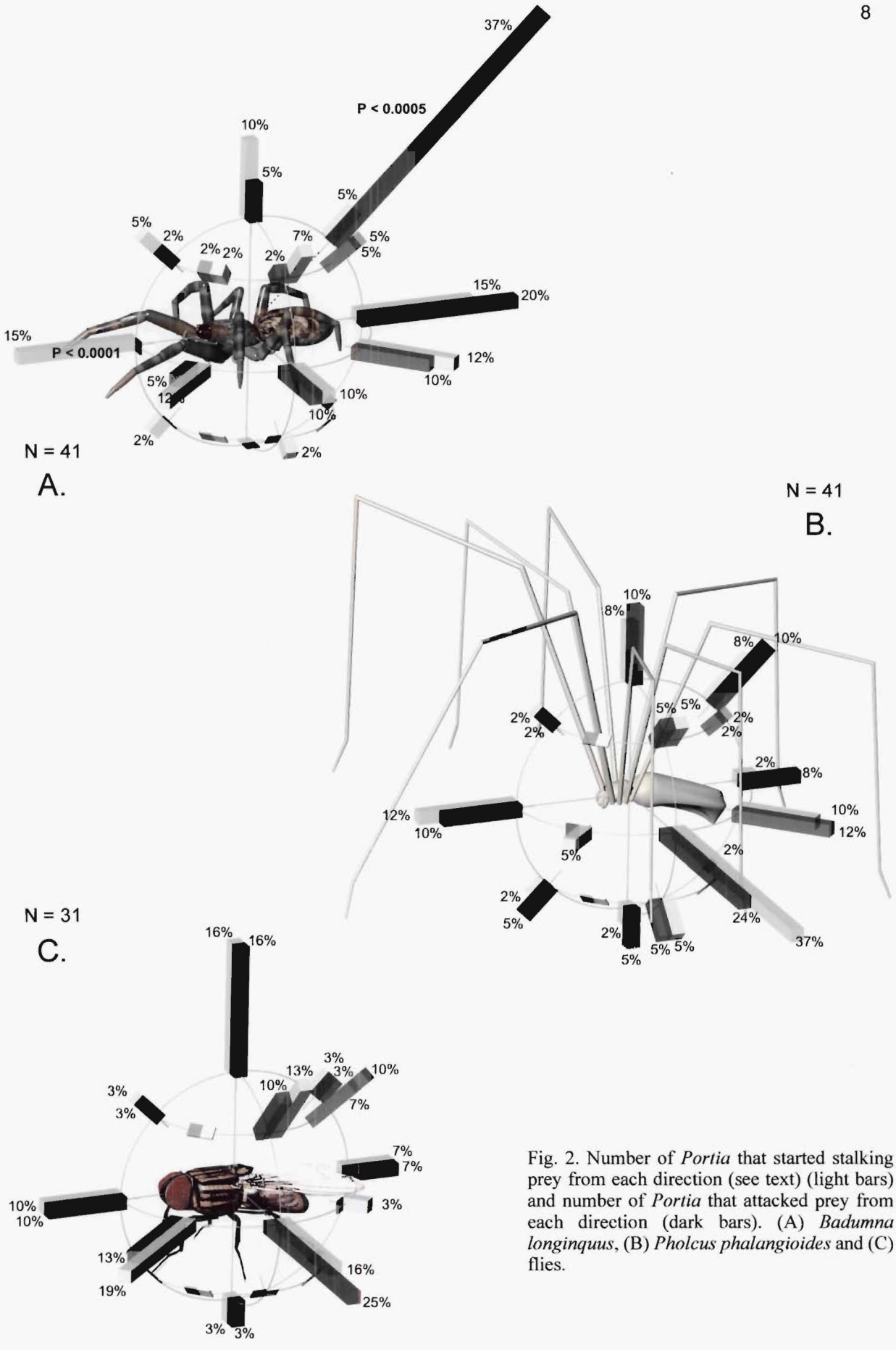

Fig. 2. Number of *Portia* that started stalking prey from each direction (see text) (light bars) and number of *Portia* that attacked prey from each direction (dark bars). (A) *Badumna longinquus*, (B) *Pholcus phalangioides* and (C) flies.

each individual *Portia* would have tended to attack from whatever the sector might have been from which it started stalking. That is, *Portia* might have been expected to have simply stalked straight towards the prey and then attacked. If this were so, the number of individuals that approached and the number that attacked from each sector would have been more or less the same.

With *B. longinquus*, most *Portia* (66%) changed sectors between beginning stalking and attacking, with the general trend being to change from more anterior sectors to more posterior ones. Of *Portia* that changed sectors, 82% did so by changing from the sector they began stalking in to a more posterior sector. The consequences of *Portia* changing sectors were most apparent in *B. longinquus*' A sector and PD sector. Every *Portia* that started to stalk from the A sector changed sectors before attacking (Fig. 2a). Although only 5% of *Portia* tested began stalking from *B. longinquus*' PD sector, significantly more (37%) attacked from that sector ($P<0.001$). This increase came about because *Portia* changed from other sectors to the PD sector. *Portia* switched sectors by manoeuvring around *B. longinquus*, waiting for *B. longinquus* to change its orientation, or a mixture of the two.

Direction of attack on Pholcus phalangioides

Results from tests with *P. phalangioides* were different than those with *B. longinquus*. For each sector, the number of *Portia* that attacked tended to be more or less the same as the number that began stalking there. The number of *Portia* that started stalking and the number that attacked was never statistically significant (Fig. 2b). However, it was not the case that each *Portia* attacked after simply approaching directly towards the prey and not switching sectors. Half of all *Portia* changed sectors between beginning stalking and attacking *P. phalangioides*, and there was no significant difference between the number of *Portia* that changed sectors with *B. longinquus* and the number that changed with *P. phalangioides*.

Portia changed between sectors by manoeuvring around *P. phalangioides*, waiting for *P. phalangioides* to change its orientation, or a mixture of the two.

In tests with *P. phalangioides*, unlike in tests with *B. longinquus*, changing sectors by *Portia* did not result in some particular sectors being favoured directions for attacks and others being avoided. Instead, attacks tended to be made by lunging through gaps between *P. phalangioides*' legs, large enough for a *Portia* to pass through. These gaps were not consistently found in any one sector, but instead tended to appear unpredictably in almost any sector. In the few cases in which *Portia* did contact *P. phalangioides*' legs during stalking, *P. phalangioides* wrapped *Portia* up with silk using its back pair of legs (Fig. 3).

Direction of attack on flies

Unlike tests with either *B. longinquus* or *P. phalangioides*, *Portia* tended to simply approach and attack *D. immigrans* or *M. domestica* from whatever sector from which stalking had begun. Only 13% of *Portia* changed sector during tests with flies, this being significantly smaller than the proportion that had changed sectors during tests with *P. phalangioides* ($P < 0.001$) or with *B. longinquus* ($P<0.001$). As a consequence of *Portia* only infrequently changing sectors during sequences with flies, the numbers of *Portia* that began stalking from each sector were almost the same as the numbers that attacked from each sector (Fig. 2c).

Body regions targeted

Portia consistently aimed its attack at the cephalothoraces of stalked spiders irrespective of the direction of attack (Fig. 4). This is illustrated by considering only those tests in which *Portia* captured the prey. In 40 out of 41 *Portia* captured *B. longinquus* by grabbing hold of this species' cephalothorax. In 39 out of 41 tests, *Portia* captured *P. phalangioides* by grabbing hold of this species' cephalothorax. *Portia* grabbed hold of the prey's abdomen in the three captures of spider prey in which the cephalothorax was not targeted. For all spider

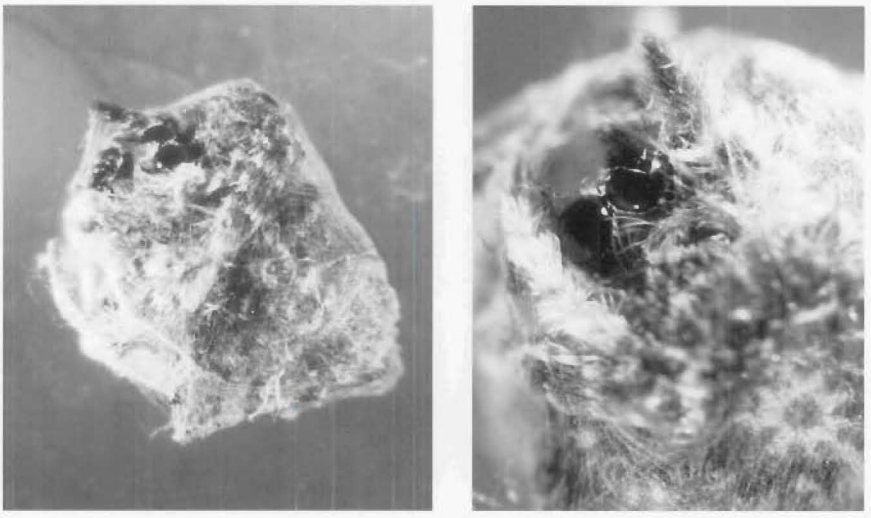

Fig. 3. *Portia* after capture by *Pholcus phalangioides*, wrapped up and unable to move.

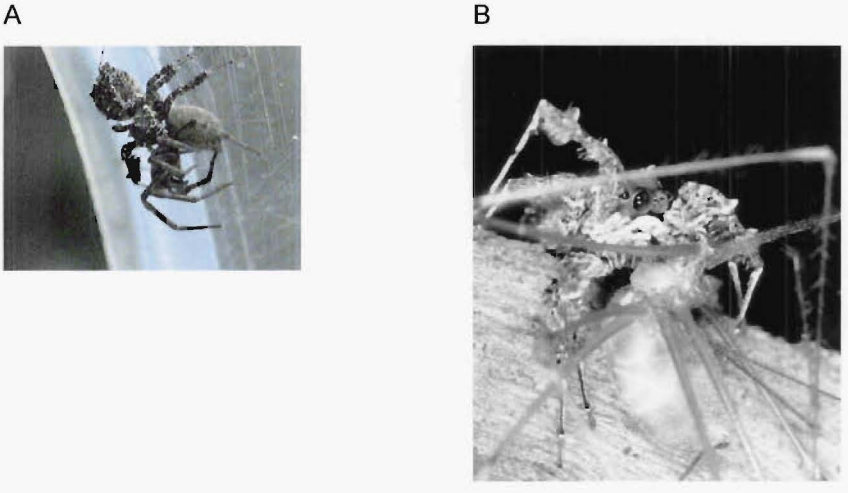

Fig. 4. *Portia* holding prey spider (A) *Badumna longinquus*, and (B) *Pholcus phalangioides* by posterior dorsal surface of cephalothorax.

prey there was little struggling when grabbed by the cephalothorax, the prey becoming quiescent with within 5 s. In contrast, the three spider prey that *Portia* grabbed by the abdomen struggled by twisting at the pedicle and intermittently flailing their legs for upwards of 30 s before becoming quiescent. Attacks on *D. immigrans* and *M. domestica* were concentrated on the front and middle regions of the body (head, 11; thorax; 19; abdomen 1). In no successful predatory sequence with either spiders or insects did any *Portia* grab hold of the prey by its legs.

Discussion

Previous studies (Jackson & Blest 1982; Wilcox et. al 1996; Li & Jackson 1996; Chapters 4-7) have established that *Portia*, using optical cues alone, discriminates between flies, conspecifics, web-building spiders, salticid prey (for *P. fimbriata*) and ants. The data presented here highlight that, when *Portia* identifies a prey, this not only triggers an immediate response but also influences a more general set of perceptual and decision-making processes in which information about the prey's orientation is used to line up an attack.

Evidence in this study shows that, with two types of spider prey, orientation is important to *Portia*. While stalking these spider prey, *Portia* frequently switched sector in order to target its attack. Not only does *Portia* use orientation information about spider prey, but how this information is used depends on the type of spider. Attacks are oriented differently depending on whether the prey is *P. phalangioides* or *B. longinquus*. When stalking *B. longinquus, Portia* changed sectors so that it could align its attack on the posterior of *B. longinquus*' carapace and avoid the anterior secotrs. When stalking *P. phalangioides*, *Portia* aligned its attacks toward any sector allowed a shot that cleared *P. phalangioides*' legs and reached the cephalothorax. During attacks on flies, orientation

seemed to be unimportant. The proximate and ultimate causes of these prey-specific attack tactics need to be clarified in future studies.

Initial hypotheses can be suggested. It may be that *Portia* uses orientation information only when the prey is dangerous and, uses the orientation information differently depending on the specific nature of the danger. In nature and the laboratory both *B. longinquus* and *P. phalangioides* sometimes kill *Portia* (unpublished data), but each of these spiders poses potentially different kinds of danger to *Portia*. *B. longinquus*' powerful legs and chelicerae would appear to make the anterior end especially dangerous to *Portia*, with the posterior end appearing to be least dangerous. It may be that neither end of *P. phalangioides* is consistently less dangerous than any other. What matters, instead, is avoiding contact with legs. *D. immigrans* and *M. domestica* probably pose little risk to *Portia,* and *Portia* appears to attack these safe prey from any sector.

Indirect evidence suggests that these hypotheses also apply to insectivorous salticids. When prey are more or less harmless insects, the primary consequences of failure during a predatory sequence may be losing a meal. This might be costly, as an insectivorous salticid that fails too often risks starvation. However, there are some insectivorous salticids that routinely prey on dangerous insects. Myrmecophagic (ant-eating) salticids are perhaps the clearest example. A carelessly aimed pounce on an ant might expose the spider to powerful mandibles, poison stings or formic acid. With few exceptions, ant-eating salticids manoeuvre to attack ants from directly in front or directly behind. However, when attacking more or less harmless insects such as flies, myrmecophagic salticids adopt no particular orientation (Li & Jackson 1996; Li et al. 1999).

Despite the different responses to orientation information in sequences with *P. phalangioides* and *B. longinquus*, *Portia* almost always struck the spider's cephalothorax. For

both of these spider prey, the cephalothorax was a relatively small target and appears to be much less accessible than either the legs or abdomen. Nevertheless, *Portia* routinely finished the attack by contacting and grabbing hold of the cephalothorax with both *B. longinquus* and *P. phalangioides*. This often meant lunging over the abdomen. When attacking *P. phalangioides*, this meant aiming accurately at the cephalothorax while at the same time avoiding contact with the legs. Successful attacks on *B. longinquus* were aimed even more precisely, usually striking a small part of the cephalothorax, the posterior dorsal surface. This part of the cephalothorax was accessible from only a restricted range of angles. This raises questions about the importance of attacking the cephalothorax.

Human behaviour suggests a reson why targeting a prey spider's cephalothorax might be advantageous for *Portia.* When a person grabs a poisonous snake, avoiding being bitten is imperative. Snake handlers routinely grip snakes from the back just below the head. Held in this way, the snake cannot reach around and bite its captor. Similarly, when its cephalothorax's posterior dorsal surface was gripped by *Portia*, *B. longinquus* appeared unable to reach *Portia* with its fangs or use its legs to dislodge *Portia.*

Another example from vertebrate behaviour may also be instructive. There have been numerous reports that leopards and lions target the necks of ungulates on which they prey (Mivart 1881; Schaller 1972; Bailey 1993). Ungulates taken by the neck appear to most often die of either suffocation when the windpipe is crushed or from damage to the spinal cord. Rapid death means there is little struggling, and therefore reduced likelihood of injury to the predator. The lion and leopard evidently achieve quick immobilisation by targeting a weak point in the prey's anatomy. The cephalothorax may be a weak spot or an 'Achilles' heel' for a spider. When the cephalothorax was grabbed by *Portia* both *B. longinquus* and *P. phalangioides* almost instantly became paralysed. In the few cases in which the abdomen was

bitten, the spider took much longer to become quiescent. Spiders have a central nervous system that is more condensed than in most other arthropods (e.g., insects). It consists primarily of two large heavily interconnected ganglia in the cephalothorax (Bullock & Horridge 1965; Babu 1985). Biting a spider on the cephalothorax may be particularly effective as a way to inject venom close to, or into, the central nervous system.

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Chapter 9. Optical cues used by *Portia fimbriata* (Araneae: Salticidae) to target specific regions of spider prey

Abstract

Portia fimbriata, an araneophagic web-invading salticid from Queensland, Australia, targets its attacks at specific region on the body of *Badumna longinquus*, a common prey spider. In an experimental study, using lures constructed from dead prey, optical cues used by *P. fimbriata* to line up attacks were investigated. Independent assessment of two factors, the presence or absence of a protruding abdomen and presence of chelicerae, appears to be critical

Introduction

Part of the predatory strategy of *Portia*, a genus of araneophagic jumping spider (Salticidae), is to adjust the orientation of attacks differently depending on the type of prey encountered (Chapter 6-8). For example, when the prey is another salticid, *Portia fimbriata* (Doleschall) attacks from the rear, grabbing hold of the salticid's posterior dorsal cephalothrorax. Freezing is an important part of *P. fimbriata*'s salticid-specific prey-capture tactic. Should a stalked salticid turn and face *P. fimbriata*, *P. fimbriata* stops approaching until it faces away again. Salticids have large anterio-median (AM) eyes, and these large eyes seem to be the critical cue by which *P. fimbriata* decides when a salticid prey is facing. *Badumna longinquus* (L. Koch), a powerful and especially dangerous web-building spider, is another spider against which *Portia* usually targets attacks on the posterior dorsal cephalothorax (Chapter 8). However, *B. longinquus* does not have large AM eyes, the orientation cues used are almost

certainly different from those used when attacking salticid prey. What these cues might be is investigated in this chapter.

Materials and Methods

Badumna longinquus, although an Australian species, is a common introduced species in New Zealand. Specimens of *B. longinquus* were collected locally as needed. A laboratory culture of *P. fimbriata* were used. Maintenance, testing procedures, cage design, terminology and conventions for describing behaviour were as in earlier spider studies (Jackson and Hallas, 1986). Testing was carried out between 0900 h and 1700 h (laboratory photoperiod 12L:12D, lights on at 0800).

For each specific test, individuals of Queensland *P. fimbriata* were chosen at random from the laboratory cultures. Each individual *P. fimbriata* tested was reared from an egg in the laboratory and fed a similar diet of insects (fruit flies and house flies: *Drosophila melanogaster* and *Musca domestica*) and spiders (various species). Before testing, hunger state was standardized by keeping each individual without prey for 5-7 days. No individual *P. fimbriata* was used more than once.

Lures made from intact females of *B. longinquus* were used as a standard. Appearance of otherwise life-like lures was systematically altered. The rationale for each alteration was to investigate the potential role as orientation cues of specific features of *B. longinquus*'s body form.

Lures were presented to *P. fimbriata* within a chamber (Fig. 1) made of transparent perspex (internal dimensions: 95 mm wide, 200 mm long and 27 mm deep). There was a circular hole (diameter 27 mm) at one end through which *P. fimbriata* could be introduced

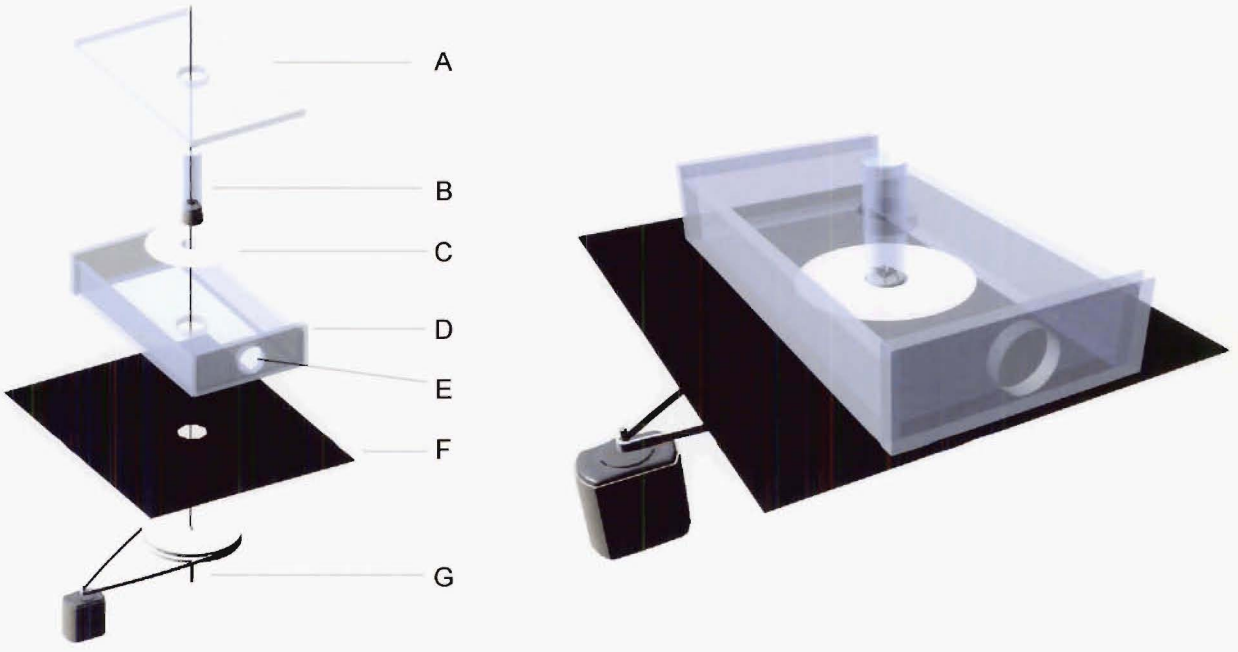

Fig. 1. Apparatus for presenting lures to *Portia fimbriata.* Left, exploded orthographic view of apparatus. Right, perspective view of apparatus set up for tests. Using a motor, lure can be rotated smoothly. Motor controls not shown. Frame for supporting turntable, motor and chamber not shown. (A) Perspex lid. (B) Lure made from dead *B. longinquus*, fixed on cork and covered by glass tube. (C) Filter paper. (D) Perspex chamber. (E) Hole for introducing *P. fimbriata*. (F) Black paper that hides turntable, motor and controls from *P. fimbriata*. (G) Turntable. on which cork with lure sits.

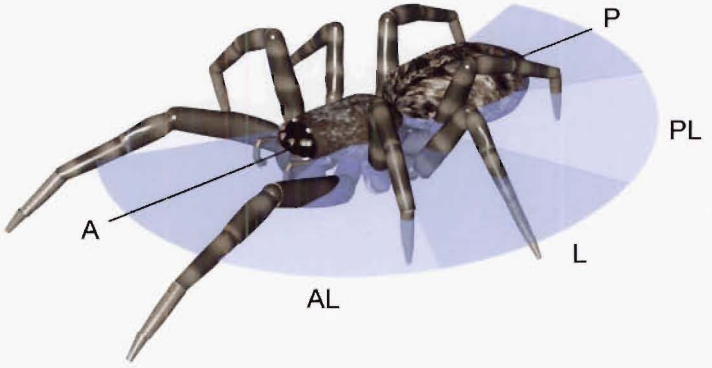

Fig. 2. Sectors that define orientation of *Badumna longinquus.* Five sectors distinguished, each covering 45° horizontal: anterior (A), anterior lateral (AL), lateral (L), posterior lateral (PL) and posterior (P).

onto the chamber floor. Centred in the chamber, 100 mm from the introduction hole, there was a glass tube (diameter 19.5 mm) covering a lure affixed atop a cork, with the cork protruding into the chamber through a hole in the chamber floor (diameter 27 mm). The top of this glass tube extended through a hole (diameter 27 mm) in the roof. With this set up, *P. fimbriata* could see, but not touch the lure.

At its base, the cork was attached to a turntable beneath the chamber. Before testing, the cork was carefully positioned so that the lure was level with the chamber floor. Using an electric motor to power the turntable, the lure could be rotated smoothly to any chosen angle. A sheet of matt black card stuck to the underside of the chamber floor hid the turntable, the motor and its controls from *P. fimbriata.* A circular piece of filter paper (diameter 80 mm) covered the floor in the centre of the chamber where the glass tube passed through a central hole (diameter 20 mm). The outer edge of the filter paper was 30 mm from the glass tube. As a precaution against possible chemical traces left by previously tested *P. fimbriata*, a fresh piece of filter paper was used for each test. The chamber was also wiped off with 80% ethanol and allowed to dry for at least 20 min between tests. Lighting was from a 100 watt tungsten filament lamp bulb 0.75 m above the chamber and fluorescent tube ceiling lights 2 m above the chamber. Light intensity was approximately 1850 lux at the chamber floor.

Before starting a test, a *P. fimbriata* (test spider) was transferred from its cage into a 30-mm long plastic tube (diameter 15 mm; stoppered at one end) and left until quiescent. The test spider was then introduced into the chamber by placing the open end of the tube at the edge of the introduction hole flush with the floor, then removing the stopper from the distal end of the tube and prodding the spider with a small brush until it walked slowly into the chamber. Occasionally *P. fimbriata* ran out of the tube and across the chamber. When this

happened, *P. fimbriata* was recaptured and returned to the small tube for reintroduction once it became quiescent again.

After a successful introduction, the lure was oriented to face 45° away from straight toward *P. fimbriata* and 'jiggled'. Jiggling was achieved by rotating the lure slowly (~1 Hz) back and forth (1-2°). Jiggling was continued until *P. fimbriata* started to stalk (defined as steady head-on movement toward the lure) and had approached to within 30 mm of the edge of the lure (i.e., *P. fimbriata* reached the edge of the filter paper). Jiggling was then stopped, the lure was rapidly rotated to face *P. fimbriata* and observation began.

With this testing procedure, a record of *P. fimbriata*'s reaction when facing the lure at different orientations could be obtained. Orientation was defined as the sector (region of the prey's body) that *Portia* faced. Each sector had a horizontal expanse of 45°. Although eight sectors were defined in this way, the number was reduced to five (Fig. 2) by pooling data from regions that were left-right mirror images of each other: anterior (A), anterior lateral (AL), lateral (L), posterior lateral (PL) and posterior (P).

Changing the lure's orientation relative to *P. fimbriata* was achieved either by rotating the lure when *P. fimbriata* was quiescent or by keeping the lure still when *P. fimbriata* moved around it (Fig. 3). Preliminary testing established that *P. fimbriata*, when pursuing live *B. longinquus*, tended to sit still and wait for the prey to move into a more favourable orientation. This tactic, which will be called 'waiting', was taken into account when designing test procedure. Whenever *P. fimbriata*'s forward motion stopped for 60 s, the lure was rotated. After rotation, the sector towards which *P. fimbriata* was oriented was always different from before. For example, if *P. fimbriata* waited while oriented toward the AL sector, the lure would be rotated, and after rotation, *P. fimbriata* might be oriented toward the centre of the P sector. However, the different sectors towards which *P. fimbriata* was oriented

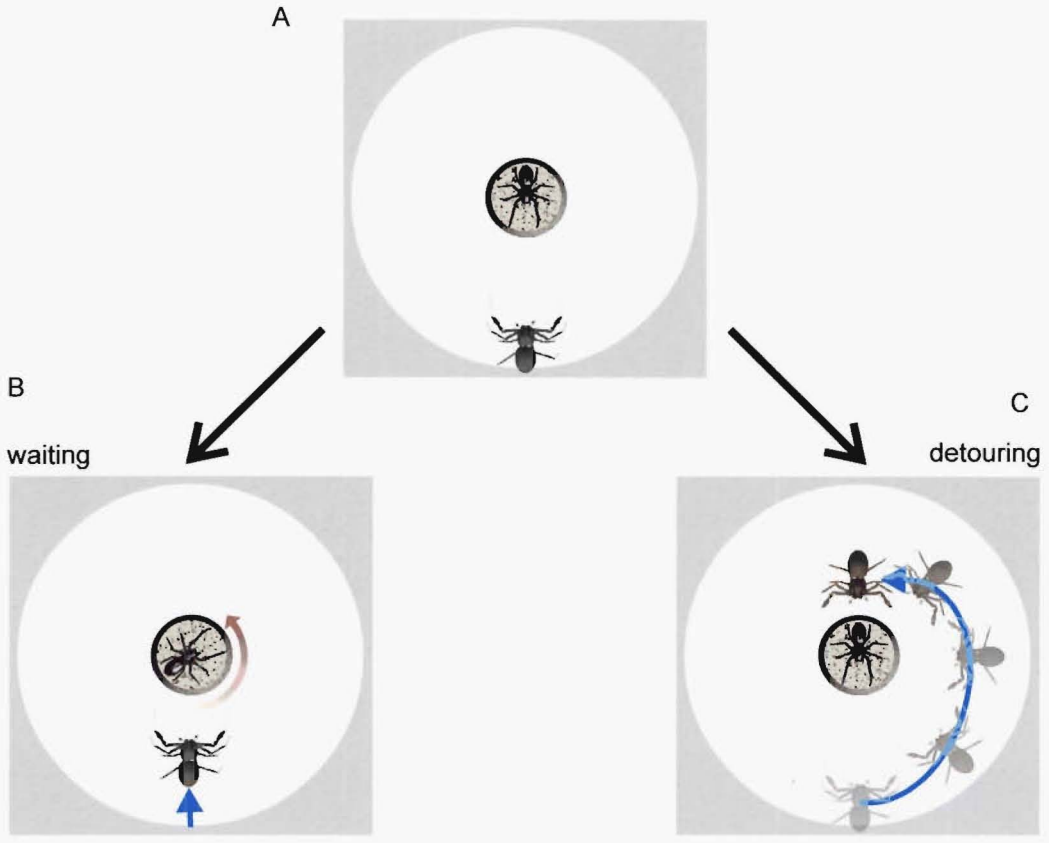

Fig. 3. Two common tactics used by *P. fimbriata* to approach lure from behind. (A) View of testing arena from above, with lure on cork and *Portia fimbriata* at edge of filter paper. (B) Waiting (*P. fimbriata* sits motionless until the lure is rotated). *P. fimbriata* approaches lure that is rotating, but does not attack until lure is facing directly away. (C) Detouring (*P. fimbriata* moves around lure while walking sideways) while lure is motionless (*P. fimbriata* spirals in towards lure's posterior end).

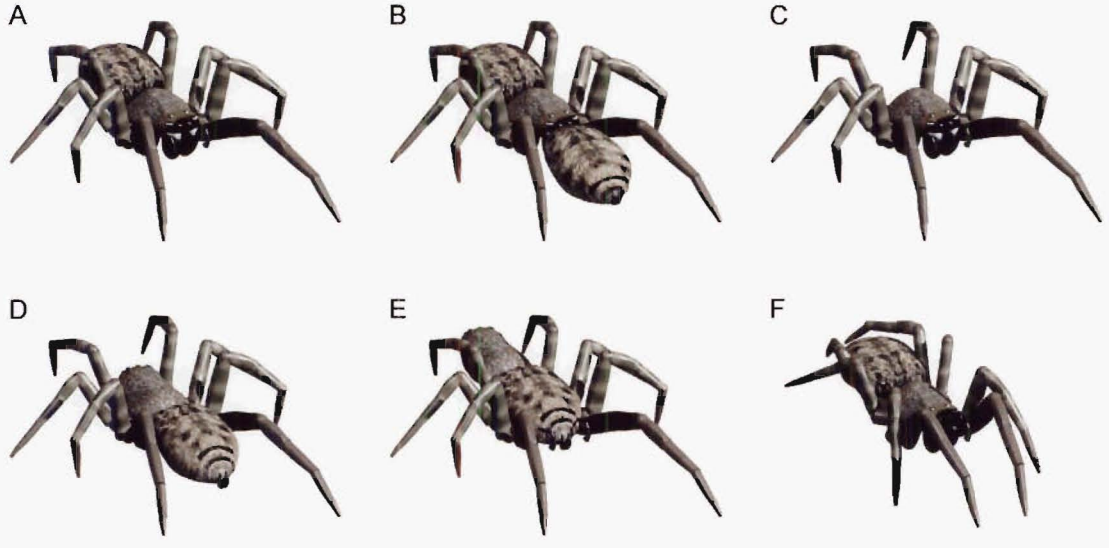

Fig. 4. Lures used in experiments. (A) Intact *Badumna longinquus* lure. (B) Lure with additional abdomen appended to its anterior cephalothorax. (C) Lure with abdomen removed. (D) Lure with carapace and abdomen placed backwards onto legs. (E) Lure with carapace and abdomen backwards and legs emerging from abdomen. (F) Intact lure with legs positioned to leave no gap at the anterior or posterior ends.

after successive periods of waiting were not chosen haphazardly. Rules were adopted that maximised the number of different parts of the lure faced by *P. fimbriata* during any given test. The first time when *P. fimbriata* waited during a test, the lure was rotated so that *P. fimbriata* was oriented toward the A sector. The second time *P. fimbriata* waited during a test (or if the first time a *P. fimbriata* that was already oriented toward the A sector waited), the lure was rotated so that *P. fimbriata* was oriented toward the PL sector. The next three times that *P. fimbriata* waited during the test, the lure was rotated so that *P. fimbriata* was oriented towards the AL, P and L sectors, respectively. While held in any particular orientation, the lure was constantly jiggled slowly back and forth (~2° at ~0.5 Hz).

Tests ended when either *P. fimbriata* touched the glass tube surrounding the lure (recorded as 'attacking' the lure) or had been exposed to all sectors of the lure without attacking, whichever came first.

Testing followed a paired design, each individual *P. fimbriata* being tested once with an intact lure and once with a modified lure. Testing order (i.e., intact lure then modified lure or modified lure then intact lure) was decided at random. *P. fimbriata* was returned to the introduction tube and placed so that the testing apparatus was out of its line of sight during the interval (5-10 min) between the first and second test. Data were analysed using the chi-square McNemar tests for significance of changes, a procedure appropriate for the paired design of the experiment (Sokal & Rohlf 1995).

Standard intact lures (Fig. 4a) were made, as in previous studies (Jackson and Tarsitano, 1993; Li and Jackson, 1996b; Chapter 3), by mounting dead, dried prey on cork disks. Experimental lures were made by systematically modifying the appearance of intact lures. A total of five different modified lures were tested (Fig. 4b-f). Experimental lures can be envisaged as asking specific questions about optical cues.

Observations

Once inside the chamber at the start of a test, *P. fimbriata* usually alternated between sitting in its typical cryptic posture (see Jackson & Blest 1982) and scanning (successively holding orientations in which its large front eyes were fixated on objects in the environment, see Tarsitano & Jackson 1997). After a few seconds, more or less, *P. fimbriata* would orient towards the lure (which was being jiggled) and begin stalking.

Lure with two abdomens

Methods

The importance of two interrelated factors was investigated: the direction in which the legs were facing and the presence of an abdomen protruding towards *P. fimbriata.* A lure with an abdomen at each end (Fig. 4b) was made. After an intact spider was fixed to a cork, a second abdomen, which was approximately the same size as the intact lure's own, was placed in between the front legs (anterior end of second abdomen pressed against the chelicerae). The direction of the lure's legs was used as a standard for assigning sectors. Therefore, at the beginning of a test, it was the appended abdomen (in front of the lure's cephalothorax) that *P. fimbriata* faced.

Results

The two-abdomen lure was typically approached and attacked directly when first presented to *P. fimbriata* (Table 1). However, with the intact lure, *P. fimbriata* typically changed to the P sector by waiting, detouring or a combination of the two, before attacking. Individual *P.*

fimbriata more often attacked from the A sector of the modified lure than from the A sector of the intact lure ($P < 0.001$). Fewer individuals switched sectors in tests in which the modified lure was used than in tests in which the intact lure was used ($P < 0.001$). Two typical sequences with the modified lure are illustrated in Table 2.

Table 1. Data from paired-test sequences with two-abdomens and intact lure (N = 19).

Percentage of individual *P. fimbriata* that	Two-abdomens lure	Intact lure	Both lures	Neither lure
Attacked from sector A	100%	5%	5%	0%
Attacked from sector A without switching sectors	95%	5%	5%	0%
Attacked from sector P	0%	95%	0%	5%
Switched sectors before attacking	5%	90%	0%	5%

Table 2. Two typical paired-test sequences (two-abdomens lure and intact lure). Each sequence described by a list, each element referring to a tactic (fig. 3) and a sector (fig. 2).

Two-abdomens lure	Intact lure	Two-abdomens lure	Intact lure
approached in A attacked in A	waited in A lure rotated to PL approached in PL detoured from PL to P attacked in P	approached in A attacked in A	detoured from A to AL detoured from AL to L detoured from L to PL detoured from PL to P attacked in P

Lure with no abdomen

Methods

After being fixed to the cork base, the abdomen of one lure (Fig. 4c) was carefully cut at the pedicel and removed. (This abdomen was used in making the two-abdomen lure).

Results

Individual *P. fimbriata* avoided the A sector of the no-abdomen and the intact lures about equally often (NS, Table 3), with sequences tending to start with *P. fimbriata* switching to more posterior sectors. However, individuals stopped changing sectors before reaching the P sector more often ($P < 0.05$) in tests in which the no-abdomen lure was used than in tests in which the intact lure was used. Individual *P. fimbriata* less often ($P < 0.001$) attacked from the P sector of the no-abdomen lure than from the P sector of the intact lure and more often ($P < 0.05$) changed to a more anterior sector when in the P sector or PL sector of the no-abdomen lure. Sometimes *P. fimbriata* detoured completely around the no-abdomen lure, eventually reaching the sector from which the detour had begun. Individuals significantly more often ($P < 0.05$) attacked from the PL sector of the no-abdomen lure than from the PL sector of the intact lure, and more failed to attack the no-abdomen lure at all ($P < 0.05$). Two typical sequences with the no-abdomen lure are illustrated in Table 4.

Table 3. Data from paired-test sequences with no-abdomen and intact lure (N = 17).

Percentage of individual *P. fimbriata* that	No-abdomen lure	Intact lure	Both lures	Neither lure
Switched from sector A to another sector	88%	100%	88%	0%
Switched from sector A to sector P	35%	82%	29%	12%
Attacked from sector P	6%	82%	0%	12%
Attacked from sector PL	59%	18%	6%	41%
Switched sectors from P or PL to more anterior sector	41%	6%	0%	53%
Failed to attack	24%	0%	0%	77%

Table 4. Two typical paired-test sequences (no-abdomen lure and intact lure). Each sequence described by a list, each element referring to a tactic (fig. 3) and a sector (fig. 2).

No-abdomen lure	Intact lure	No-abdomen lure	Intact lure
waited in A lure rotated to PL approached in PL detoured from PL to P retreated in P detoured from P to PL attacked in PL	waited in A lure rotated to PL approached in PL detoured from PL to P attacked in P	waited in A lure rotated to PL approached in PL retreated in PL waited in PL lure rotated to AL retreated in AL waited in AL lure rotated to P retreated in P detoured from P to PL detoured from PL to L retreated in L ignored lure	retreated in A waited in A lure rotated to PL detoured from PL to P attacked in P

Lure with legs and palps facing backwards

Methods

One lure was made by carefully cutting away an intact lure's upper (dorsal) cephalothorax (incision below the carapace but above the legs). The excised carapace, had the abdomen and chelicerae still attached. The legs and palps were still attached to the lower (ventral) cephalothorax. Next the excised carapace was turned around and placed backwards onto the lower section of the cephalothorax (Fig. 4d). The resulting lure resembled the intact lure except that its legs were back to front (i.e., in reference to the dorsal body, legs I were posterior to legs IV). Palps were no longer visible, being covered by the abdomen. Naming of sectors corresponded to ventral body and normal leg direction. This meant that the end of the lure with the abdomen protruding was named the A sector.

Results

Individual *P. fimbriata* more often ($P < 0.001$) attacked from sector A of the reversed-legs lure than from sector A of the intact lure (Table 5). In tests using the intact lure, all *P. fimbriata* switched from the A sector at the beginning of tests, eventually attacking from a sector other than the A sector. However, in tests in which the reversed-legs lure was used, 47% of attacks were made from the A sector at the beginning of a test ($P < 0.01$). Two typical sequences with the reverse-legs lure are illustrated in Table 6.

Table 5. Data from paired-test sequences with reversed-legs and intact lure (N = 19).

Percentage of individual *P. fimbriata* that	Reversed-legs lure	Intact lure	Both lures	Neither lure
Attacked from sector A	90%	0%	0%	11%
Switched sectors before attacking	53%	100%	53%	0%

Table 6. Two typical paired-test sequences (reverse-legs lure and intact lure). Each sequence described by a list, each element referring to a tactic (fig. 3) and a sector (fig. 2).

Reversed legs lure	Intact lure	Reversed legs lure	Intact lure
detoured from A to AL detoured from AL to L detoured from L to PL detoured from PL to P waited in P lure rotated to PL detoured from PL to L detoured from L to AL detoured from AL to A attacked in A	waited in A lure rotated to PL detour to P attacked in P	approached in A attacked in A	waited in A lure rotated to PL detoured from PL to P attacked in P

Legs backwards and emerging from abdomen

Methods

The effect of having the carapace protrude like an abdomen (Fig. 4e) was investigated. A lure was made similarly to how the reversed-legs lure was made except that the excised carapace

and abdomen were placed further back so that the legs and palps emerged from underneath the abdomen and the carapace protruded out the back. The palps were clearly visible sticking out from under the abdomen. The chelicerae were clearly visible on end of the carapace. Sector A was at the end with the palps and abdomen.

Results

When the legs-under-abdomen lure was turned to face *P. fimbriata* at the beginning of tests, it was treated much the same as the intact lure. *P. fimbriata* never attacked in sector A of either lure (Table 7). With both the legs-under-abdomen lure and the intact lure, individuals tended to switch sectors until they reached the P sector (NS). However, individuals less often ($P < 0.001$) attacked from the P sector of the legs-under-abdomen lure than from the P sector of the intact lure and more often ($P < 0.001$) changed to a more anterior sector when in the P sector or PL sector of the legs-under-abdomen lure. Some *P. fimbriata* were reluctant to attack (i.e., they switched into and out of the P sector multiple times). A significant number of individuals (44%) failed to attack the legs-under-abdomen lure at all ($P < 0.01$). The intact lure was always attacked. Two typical sequences with the legs-under-abdomen lure are illustrated in Table 8.

Table 7. Data from paired-test sequences with legs-under-abdomen and intact lure (N =18).

Percentage of individual *P. fimbriata* that	legs-under-abdomen lure	Intact lure	Both lures	Neither lure
Attacked from sector A	0%	0%	0%	100%
Switched from sector A to sector P	67%	78%	56%	11%
Attacked from sector P	11%	94%	11%	6%
Switched sectors from P or PL to more anterior sector	94%	6%	6%	6%
Failed to attack	44%	0%	0%	56%

Table 8. Two typical paired-test sequences (legs-under-abdomen lure and intact lure). Each sequence described by a list, each element referring to a tactic (fig. 3) and a sector (fig. 2).

Legs-under-abdomen lure	Intact lure	Legs-under-abdomen lure	Intact lure
waited in A lure rotated to PL approached in PL detoured from PL to P retreated in P detoured from P to PL approached in PL retreated in PL waited in PL lure rotated to AL waited in AL lure rotated to P detoured from P to PL attacked in PL	waited in A lure rotated to PL detoured from PL to P attacked in P	waited in A lure rotated to PL detoured from PL to P detoured from P to PL detoured from PL to L detoured from L to AL detoured from AL to A retreated in A ignored lure	waited in A lure rotated to PL detoured from PL to P attacked in P

Lure with legs shielding anterior and posterior

Methods

The hypothesis tested is that gaps between legs provide cues for lining up attacks and that these cues act independently of cues provided by features from the carapace and abdomen. For investigating this hypothesis a lure with legs shielding the abdomen and the front of the carapace was made (Fig. 4f). This lure was an intact *B. longinquus*. However, unlike the standard intact lure, all its legs were repositioned so that they covered up the wide gaps

between legs that are visible to *P. fimbriata* in the A and P sectors of the standard intact lure. What is more, by repositioning the legs in this way, a new gap was created at the sides (L sector).

Results

Individual *P. fimbriata* less often ($P < 0.001$) attacked from the P sector of the leg-gaps-at-sides lure than from the P sector of the intact lure (Table 9) and significantly more often waited at the P sector or detoured away from the P sector of the leg-gaps-at-sides lure ($P < 0.005$). Despite the gaps left at the sides by the legs, attacks never came from the L sector. Individuals more often ($P < 0.001$) failed to attack the leg-gaps-at-sides lure than the intact lure. Two typical sequences with the leg-gaps-at-sides lure are illustrated in Table 10.

Table 9. Data from paired-test sequences with leg-gaps-at-sides and intact lure (N = 18).

Percentage of individual *P. fimbriata* that	Leg-gaps-at-sides lure	Intact lure	Both lures	Neither lure
Attacked from sector P	11%	78%	11%	22%
Attacked from sector L	0%	0%	0%	100%
Switched sectors from P sector	56%	6%	6%	33%
Failed to attack	39%	0%	0%	61%

Table 10. Two typical paired-test sequences (leg-gaps-at-sides lure and intact lure). Each sequence described by a list, each element containing a tactic (fig. 3) and a sector (fig. 2).

Leg-gaps-at-sides lure	Intact lure	Leg-gaps-at-sides lure	Intact lure
waited in A lure rotated to PL approached in PL detoured from PL to L waited in L lure rotated to FL detoured from FL to L detoured from L to PL waited in PL lure rotated to P waited in P test ended	waited in A lure rotated to PL detoured from PL to P attacked in P	detoured from A to AL detoured from AL to L detoured from L to PL detoured from PL to P detoured from P to PL attacked in PL	detoured from A to AL detoured from AL to L detoured from L to PL detoured from PL to P attacked in P

The effects of a protruding 'abdomen'

At the beginning of tests in which the reversed-legs lure was used, *P. fimbriata* faced the lure's protruding abdomen. With the legs-under-abdomen lure, *P. fimbriata* also faced the abdomen at the beginning of tests, but the abdomen did not protrude forward beyond the base of the legs. Comparing individual *P. fimbriata* that did not attack from the A sector of the intact lure but did with the modified lure, we find that significantly more ($P < 0.001$; test of independence, chi-square; $N = 37$) attacked from the A sector of the reversed-legs lure (abdomen protruding, Table 5) than from the A sector of the legs-under-abdomen lure (abdomen not protruding, Table 7).

Discussion

P. fimbriata appears to use optical cues alone to determine *B. longinquus*' orientation. Two cues provided by the anterior of *B. longinquus* and one provided by the protruding abdomen are implicated by the experimental findings.

P. fimbriata tended not to attack the anterior or the posterior end of the legs-under-abdomen lure (Fig. 4e), suggesting an inhibitory effect of some feature of the typical front end of *B. longinquus*' carapace. Chelicerae are prominent features of the front end of an intact *B. longinquus* suggesting that detection of chelicerae serves for *P. fimbriata* as a cue for not attacking. A difficulty with this hypothesis is that *P. fimbriata* also avoided attacking from the A sector of the legs-under-abdomen lure. Optical cues from chelicerae may have inhibited *P. fimbriata* from attacking from the P sector, but when oriented toward the A sector the chelicerae were out of *P. fimbriata*'s line of sight. Likewise, individuals less often

attacked from the P sector of the no-abdomen lure (Fig. 4c) than from the P sector of the intact lure despite chelicerae not being in view when oriented toward the P sector. However, with both the legs-under-abdomen lure and the no-abdomen lure, the end of the lure without the chelicerae also had no protruding abdomen. The effects of having the abdomen protrude or not protrude were investigated by comparing *P. fimbriata*'s behaviour at the beginning of tests with the legs-under-abdomen lure and the reversed-legs lure. That the reversed-legs lure, but not the legs-under-abdomen lure, tended to be attacked from the A sector implicates that the abdomen's position relative to the legs, rather than any specific feature of the abdomen itself (e.g., patterning or shape), as the cue.

Apparently both the presence of chelicerae (or some other less prominent feature of the front of the carapace) and the absence of an abdomen (i.e., absence of a large body part) protruding from between the legs provide alternative cues, on the basis of either of which *P. fimbriata* can ascertain that it is facing the anterior of *B. longinquus*. Having two alternative cues that indicate the anterior end of *B. longinquus* may be indicative of the importance to *P. fimbriata* of having a failsafe mechanism of avoiding encountering this end during predation.

When identifying the posterior end of *B. longinquus*, *P. fimbriata* appears also to rely on cues from the abdomen. With the two-abdomens lure (Fig. 4b) and the reversed-legs lure (Fig. 4d) *P. fimbriata* began tests facing a protruding abdomen. With both these lures attacks came typically at the beginning of tests and from in the A sector. *B. longinquus*' abdomen protruding directly toward *P. fimbriata* seems to inform *P. fimbriata* that the prey is aligned ready for approach and attack.

B. longinquus' protruding abdomen may also provide cues that influence *P. fimbriata* when not in the P sector. When tested with the intact lure, *P. fimbriata* tended to switch sectors until reaching the P sector. However, when tested with the no-abdomen lure (Fig. 4c),

the same individual *P. fimbriata* tended to stop switching sectors before reaching the P sector. This suggests that cues provided by the abdomen indicate to *P. fimbriata* the direction in which it will need to move to reach *B. longinquus*' posterior. That cues from the abdomen come from the abdomen's position relative to the legs (i.e., that it protrudes), rather than its shape or patterning, is suggested by how *P. fimbriata* tended to switch sectors until they reached the P sector both when tested with the intact lure and when tested with the legs-under-abdomen lure (carapace protrudes).

The direction in which the legs slanted did not seem to reveal to *P. fimbriata B. longinquus*' orientation. For example, the reversed-legs lure tended to be treated as if it were an intact *B. longinquus* that was facing away from *P. fimbriata*, despite leg positioning being typical of a *B. longinquus* that was facing toward *P. fimbriata*.

The position of gaps between legs did not appear to be a cue used by *P. fimbriata* for lining up attacks on *B. longinquus*. Gaps between legs that are large enough for *P. fimbriata* to pass through are typically found in *B. longinquus*'s A sector and P sector, and this was the case with the intact lure. With the leg-gaps-at-side lure (Fig. 4f) these gaps were moved to be in the lure's L sector. Yet *P. fimbriata* never oriented attacks through these large gaps between the legs. However, with this lure *P. fimbriata* also tended to avoid attacking from the P sector, suggesting that although a large gap between legs is not itself used as an attack orientation cue for indicating where to attack, absence of large gaps between legs inhibit attacks even when other cues (i.e., a protruding abdomen) indicate that *P. fimbriata* is in the P sector. Experimental investigation, using modified lures, would be useful for clarifying attack-orientation cues when *Pholcus phalangioides* are the prey. When attacking these long-legged spiders, *Portia* appears to be strongly influenced by gaps (Chapter 8)

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Chapter 10. Discussion

This thesis is a step toward a larger aim of using *Portia* to investigate cognitive mechanisms. Rather than highlighting any specific conclusions from the thesis, the objective in this final chapter is to discuss a preliminary framework for guiding future studies.

Cognition

Simply establishing that studying *Portia*'s behaviour might be significant for understanding animal cognition already goes a long way toward defining a framework for future studies (see Chapter 2). Complex, flexible behaviour, problem-solving ability, learning by trial and error and planning ahead all raise questions that fit into existing cognitive frameworks such as those devised by Dennett (1995, 1996), Dukas & Real (1993) and Mitchell (1986) (see Wilcox & Jackson 1998). However, the meaning of the word 'cognition' is often hard to pin down.

Along with 'cognition' there are a number of terms that tend to be used together but do not appear to be easy to define. 'Thinking', 'intelligence', 'consciousness', 'awareness', 'mental' and 'mind' are examples. Some more specific terms include learning, planning, language, imagination, self-awareness, cognitive-maps and so on. The way these terms are used can often appear frustratingly vague and shifting. Part of the problem may be in how the same terms are often used in multiple contexts within science and philosophy. When used in reference to humans, 'cognition' may often imply attributes that are not necessarily applicable when 'cognition' is used in reference to mental processes of non-human species (Beer 1998). Even when applied to non-human animals 'cognition' tends to carry different unstated meanings depending on the type of non-human animal. When discussing 'cognition' in animals as distantly related as, for instance, chimpanzees (primates) and *Portia* different implied meanings of the word have a potential for causing significant misunderstanding. It can be argued that looking for

a highly precise definition is misguided for many of the most basic topics investigated in science. 'Cognition' may be rather like 'behaviour', 'life', 'communication' and so forth: something where definitions need to be highly generalized and where we are better off not attempting to tie ourselves to an overly explicit definition (see Dennett 1998). For many, 'cognition' is a term that is conveniently vague. However, with 'cognition' the definition problem may not be that easy to sweep away. There appears to be a serious danger for researchers in this field talking past each other, rather than addressing mutually perceived questions.

The Concise Oxford Dictionary of Zoology (Allaby 1991) defines cognition as, "mental processes that are presumed to be occurring within an animal but which cannot be observed directly." This simple definition may be a good starting place, but it leaves undefined another critical term, 'mental', which may approximate being little more than a synonym for 'cognitive'. That cognition involves processes, whatever they may be, and that these processes can not be observed directly is probably rightly emphasised. Deciding what non-directly-observable 'mental' processes might be appears to be something of an impasse. Clearly it is time to move beyond Descartes (1637) and the notion of a discontinuity between 'physical' and 'mental'. Somehow, while avoiding this dead-end attitude, we need a way of addressing the notion of physical space (e.g., eyes, neurons, muscles), where things are directly observable, and mental space. Although at some level cognition involves processes that are occurring in physical space (i.e., inside the animal's body), it may not be possible for us to describe or understand cognition at this level. Talking about mental space may be a concession that must be made if we are to make the types of complex behaviour generated by millions of interacting cellular processes intelligible. In this case, 'cognition' would appear to be a term for processes that take place in mental space. The key point is that mental space is an abstract notion of space, rather akin to cyberspace, or space

in virtual reality. This is not exactly a definition of 'cognition', or even close to one, but it may be the direction in which we might usefully look for one.

Depiction of processes in salticid mental space

A major aim of recent behavioural research on *Portia* has been to investigate 'how *Portia* knows when to do what.' (introduction, Chapter 2). This is not so very new as an emphasis in salticid research. Although detailed behaviour studies on *Portia* began only in the early 1980s (e.g., Jackson & Blest 1982; Jackson 1982), the question of how salticids in general know when to do what goes back to Peckham and Peckham (1887). Heil (1936), Crane (1949), Drees (1952) and Land (1972) can also be envisaged as having worked on this question. However, over the past 110 years there has been a significant shift in the exact approaches taken and the kinds of answers expected (Fig. 1).

At the dawn of the eighties, salticids were generally portrayed as fairly simple animals that relied almost entirely on simple, pre-programmed more or less reflex-like responses to specifiable stimuli. A simple decision tree probably comes close to depicting the internal algorithm that most researchers would have accepted as how salticids ran much of their normal day-to-day lives (Fig. 2). Although flexible enough to produce behaviour that on the surface appears similar to that of a predatory mammal (Land 1974), this decision tree algorithm is simple enough to be housed in a small brain in the small arachnid body of a salticid. Perhaps the broadest consequence of the past 20 years of research on salticid behaviour has been to show how unsuitable a decision-tree algorithm is for describing the behaviour of salticids. Although a decision-tree algorithm seems too simple to require explanations framed in terms of cognition, for *Portia* in particular something else is needed for making sense of behaviour. Call it 'cognition' or call it something else, it will not be a simple decision-tree algorithm. What we need is an algorithm that can handle *Portia*'s enormous behavioural repertoire (Fig. 3), that can

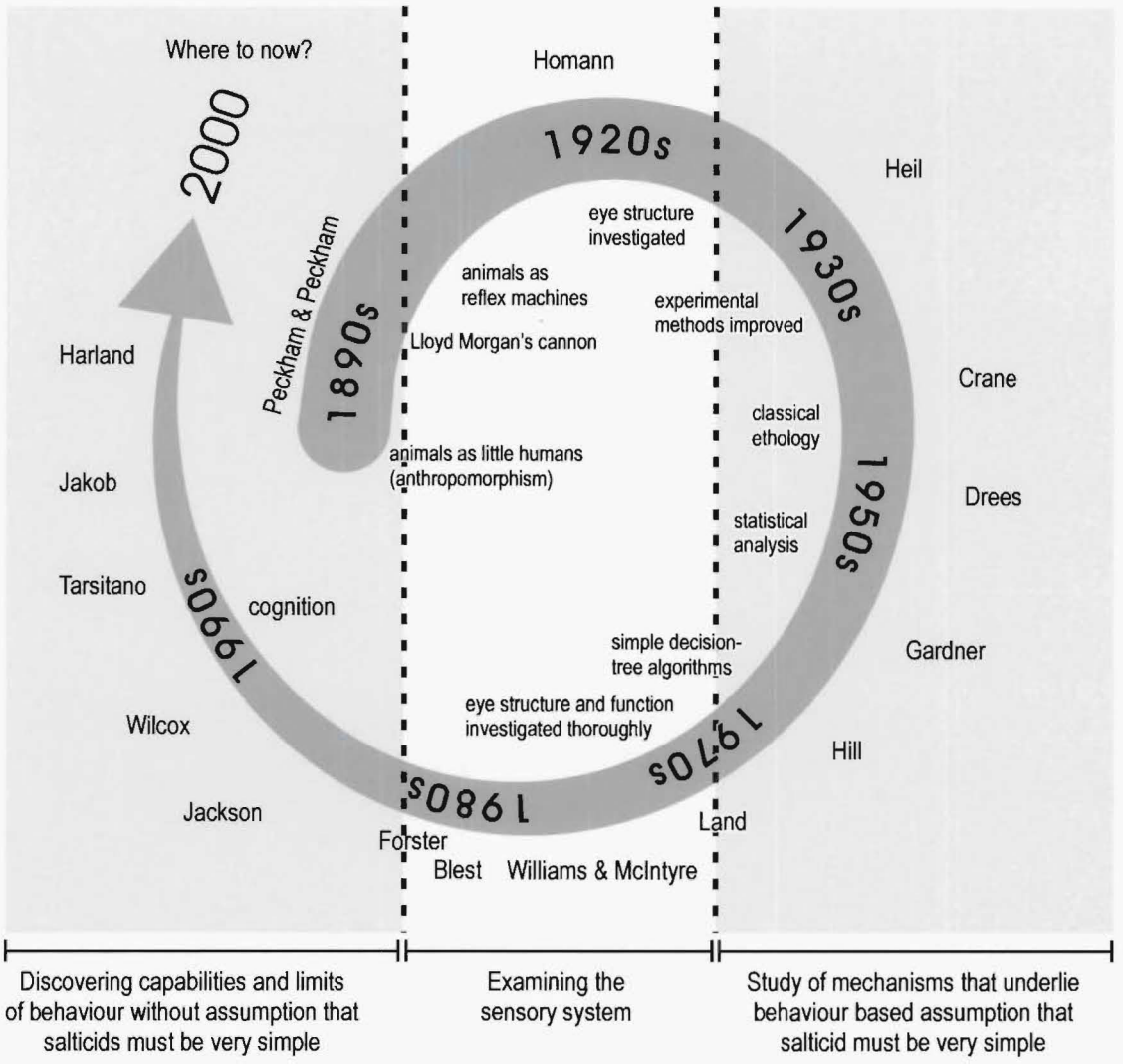

Fig. 1. Summary of research on salticid behaviour during past 110 years. Directly or indirectly, prominent researchers (listed on outside of time line) were motivated by the question "how does a salticid know when to do what". How expectations and assumptions about the answer to this question, along with research methods, evolved is on the inside of the time line.

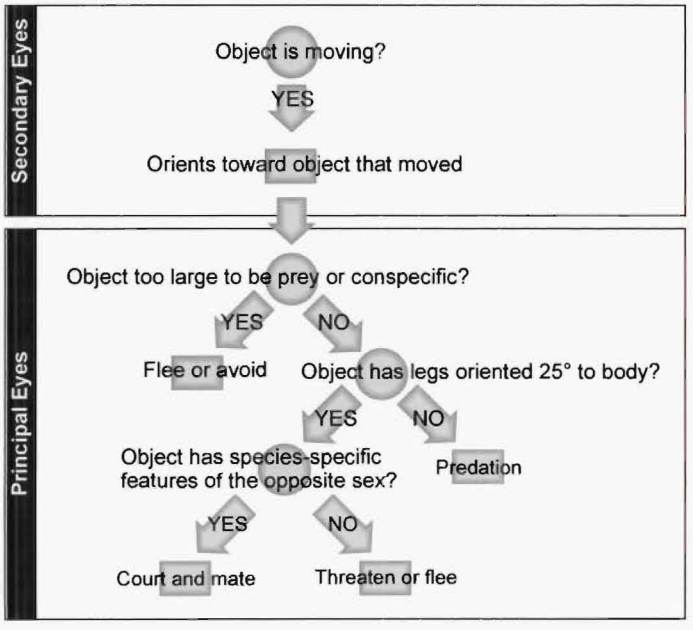

Fig. 2. Depiction of decision-tree algorithm representing a generalized internal program for salticids based on research up until the 1980s.

Fig. 3. What *Portia* spp. do. Depiction of diversity of alternative tactics in *Portia*'s repertoire. Selected tactics not listed in any particular order. During predatory sequences *Portia* tends to switch back and forth between tactics and one tactic may be influenced by others. Each tactic has its own set of cues and influences.

at some level be grounded in physical space (e.g., neurons) and yet can depict *Portia*'s internal program in an easy to follow way.

In a decision tree, each fork represents a choice that leads down a branch to one endpoint or another. What choice is made at each fork depends on the detection of a specific cue, and a specific cue can be either present (animal chooses 'yes' branch) or absent (animal chooses other branch). In Chapter 6 the cues that influence *Portia*'s tendency to stalk salticid prey were investigated. It was shown that different cues can sometimes independently influence the same choice (i.e., to stalk or not to stalk), and different cues can also influence any given choice by different amounts. In particular, a prey's legs provided cues that had a big influence on stalking tendency, but the carapace and abdomen of the prey also provided cues, although each of these had only a small influence. A 'yes-no' decision tree might be designed to represent the findings from Chapter 6, but it would no longer be exactly simple. As we learn more, the problems are likely to get rapidly worse. In general, it appears to be inadequate to express algorithms for *Portia*'s behaviour in terms of a series of "if" statements joined together to form simple discrete decision trees.

In Chapter 6 it was suggested that a more appropriate way of expressing an algorithm for *Portia* might be to base it on interactions between a set of independent perceptual processes and a set of response processes. In this model each perceptual process has the task of identifying a specific cue, and each response process mediates different predatory tactics. Each process can influence others by activating them. Activated processes can then activate other processes and so on. In the study presented in Chapter 6, *Portia* would either stalk a lure or not, and this was represented by whether or not a response process had been activated (by other processes). Activation of a response process for stalking could happen via more than one pathway in mental space, the exact pathway being used in any specific instance being non-deterministic. Being non-

deterministic is an important feature of this kind of algorithm and being non-deterministic may also be important for describing cognition in general.

In his book on human consciousness, Minsky (1985) suggested some similar ideas. He likened the human mind to a human society populated with thousands of individual processes. Each process had its specific task and motivations, with conscious thought being the result of communication between some unspecified large number of these processes. Minsky called his processes 'agents' and although the specific processes operating within salticid mental space are almost certain to be very different from those operating in human mental space, Minsky's general idea might be applicable to a salticid mind. At this stage, the idea of agent-based algorithms applying to cognition in *Portia* is no more than that (i.e., only an idea), but it would be interesting to see where this might lead in future study.

Sensory information

Another approach to investigating how *Portia* knows when to do what is clarify what information influences decisions. Whether agent based or not, we need an algorithm pertaining to how *Portia* makes decisions based on information. For explaining *Portia*'s behaviour it will be critical to understand what kinds of information influence *Portia*'s decisions. The information that Portia might use can be envisaged as coming from two crude categories depending on whether it is derived from an internal or an external source.

The nature of internal information and how it is generated may come partly from physiological studies (e.g., clarifying hunger level and sexual drive). Internal information might also be envisaged as derived from genetically preprogrammed tendencies or from inclination derived from learning and experience, and for this distinction behavioural studies are needed in which earlier experience is manipulated or controlled..

Sensory systems are the source of external information. In salticids, vision is generally considered to be the most important sensory system. This system was reviewed in Chapter 2. However, for understanding vision and how it relates to cognition, studying the eyes alone is not enough. What is fed from the eyes into the perceptual processes in *Portia*'s mental space must be refined so that meaningful information can be discriminated from background noise. Although eyes and other sense organs themselves play a role in filtering out noise from the environment, the perceptual processes in *Portia*'s internal program in the end determine what information is available for shaping behaviour. These perceptual processes, not being directly observable, must be investigated by means of behavioural studies (Chapters 4-9).

Future directions

There are four lines of study that appear especially promising for understanding of cognition in *Portia*. First, there is development of algorithms based on agents. One way of doing this is with robotics. One of my long-term goals (or dreams) is to design a robot control system that can operate in the real world, dealing with real-world environmental noise, and generally perform cognitively comparably to a real *Portia*. Achieving an operational robot would provide especially strong evidence that we have understood the underlying algorithms.

Second, more study of perceptual cues is needed. For this line of research the VLPS (Chapter 3) is a new and powerful tool that needs to be taken further. Current studies have concentrated primarily on discovering what cues are used to discriminate different classes of prey. Besides more in-depth studies of this type, studies are also needed on what cues from the non-prey environment might guide activities such as navigation, nest site choice and web-building.

Third studies are needed on the movement patterns of the principal eyes (see Chapter 2). Land (1969) suggested that the intricacy of eye-tube movement may be a critical part of the mechanism by which the salticid perceives shape and form. Precisely how this might be achieved is poorly understood. This may be the urgently needed area for future work on salticid visual perception. That the salticid, by adopting particular patterns of eye-tube movement, may be searching for specific identifying features of the object being viewed is a hypothesis that needs testing. The salticid's eyes have behaviour and this behaviour may uniquely in salticids reveal how visual perception is achieved. Yet, 30 years onwards, Land's pioneering study is still almost everything we know about salticid eye-tube movement. Although methodological difficulties, including the need for a specialised opthalmoscope with which to look inside the eyes of salticids, have probably discouraged further research the difficulties are not insurmountable (see Appendix B).

Finally, moving beyond processing external information, studies are needed on *Portia*'s internal programs.

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Appendix A. Eight-legged cats: A review on recent work on Portia and other jumping spiders (Araneae: Salticidae)

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Abstract

Recent work on the eyes and vision-guided behaviour of jumping spiders (Salticidae) is reviewed. Special attention is given to *Portia*. The species in this African, Asian and Australian genus have especially complex predatory strategies. *Portia*'s preferred prey are other spiders, which are captured in sequences based on making aggressive-mimicry web signals, problem solving and planning. Recent work has used *Portia* to study cognitive attributes more often associated with large predatory mammals such as lions and rarely considered in studies on spiders. In salticids, complex behaviour and high-spatial-acuity vision are tightly interrelated. Salticid eyes are unique and complex. How salticid eyes function is reviewed. Size constraints are discussed.

Introduction

When studying spiders, salticids are not easily mistaken for anything else. In English, the common name for salticids is 'jumping spiders' and many are indeed phenomenal leapers. However, jumping alone is not what distinguishes salticids from other spiders. Some other spiders can jump, but only salticids make accurate vision-guided leaps on to prey and other targets. What makes salticids special is their unique, complex eyes and acute eyesight, not leaping prowess. Salticids have large anterior medial eyes that give them an almost catlike appearance. No other spider has eyes like these

and no other spider has such intricate vision-guided behaviour. The feline analogy is more than superficial (Land 1974), and a better common name for salticids would probably be 'eight-legged cats'.

Like a cat, a salticid uses more than its eyesight during prey-capture sequences. Chemoreception and other modalities also play a role. However, like a cat, and unlike any other spider, a salticid locates, tracks, stalks, chases down and leaps on active prey, with all phases of these predatory sequences being under optical control (Forster 1982). Using optical cues, salticids discriminate between mates and rivals, predators and prey, different types of prey, and features of non-living environment (Crane 1949; Drees 1952; Heil 1936; Jackson & Pollard 1996; Tarsitano & Jackson 1997). In terms of spatial acuity, no other spider can see this well.

Resemblance between cats and salticids may go beyond having good eyesight. Animal intelligence, animal cognition and related topics, although long neglected by scientists studying behaviour, are now being taken seriously (Gallistel 1992; Griffin 1984). For cats, especially big cats such as lions, many scientists might be ready to concede that these topics are relevant, but cognition is not a conventional topic in spider studies. There may be compelling reasons for the traditional portrayal of spiders as simple, instinct-driven animals (Bristowe 1958; Savory 1928), and the very notion of discussing 'spider minds' might seem comical, if not scientifically disreputable.

Here we will review recent work on salticids that challenges conventional wisdom. Of the salticids that are well studied to date, those with the highest optical spatial acuity (Williams & McIntyre 1980) and most complex behaviour (Jackson & Pollard 1996) are species in the genus *Portia* (Wanless 1978). Our review focuses on *Portia*.

Portia's predatory strategy

Most salticids prey primarily on insects caught by actively hunting instead of by building webs (Richman & Jackson 1982), but *Portia* not only hunts out in the open but also builds a prey-catching web. There is more. *Portia* invades the webs of other spiders where it feeds on other spiders' eggs, on insects ensnared in their webs and on the other spiders themselves (Fig. 1). *Portia* is also unusual in appearance, not really looking like a spider at all, or even an animal, but instead like detritus in a web (Jackson 1996; Jackson & Blest 1982a).

Hunting in another spider's web is dangerous and *Portia* has evolved complex, flexible behaviour that minimises risk. Instead of simply stalking or chasing down its victim, *Portia* generates aggressive-mimicry web signals (Tarsitano *et al.* in press). *Portia*'s preferred prey (Li *et al.* 1997), web-building spiders, have only rudimentary eyesight (Land 1985) and rely primarily on interpreting web signals (Foelix 1996). Web signals are the tension and movement patterns conveyed through silk of the web, with the spider's web being almost literally a sense organ (Witt 1975).

Portia makes aggressive-mimicry signals by manipulating, plucking and slapping web silk with any one or any combination of its eight legs and two palps. Each appendage can move in a great variety of ways, and movement patterns of any one appendage, however complex, can be combined with different movement patterns of any number of the other appendages (Jackson & Blest 1982a; Jackson & Hallas 1986). On top of all the signals made possible by moving legs and palps, *Portia* also makes signals by flicking its abdomen up and down, and abdomen movement can also be combined in various ways with the different patterns of appendage movement. The net effect is that *Portia* has at its disposal a virtually unlimited array of different signals to use on the webs of other spiders (Jackson & Wilcox 1993a).

Figure 1. *Portia* feeds on *Pholcus phalangioides*, a long-legged web-building spider.

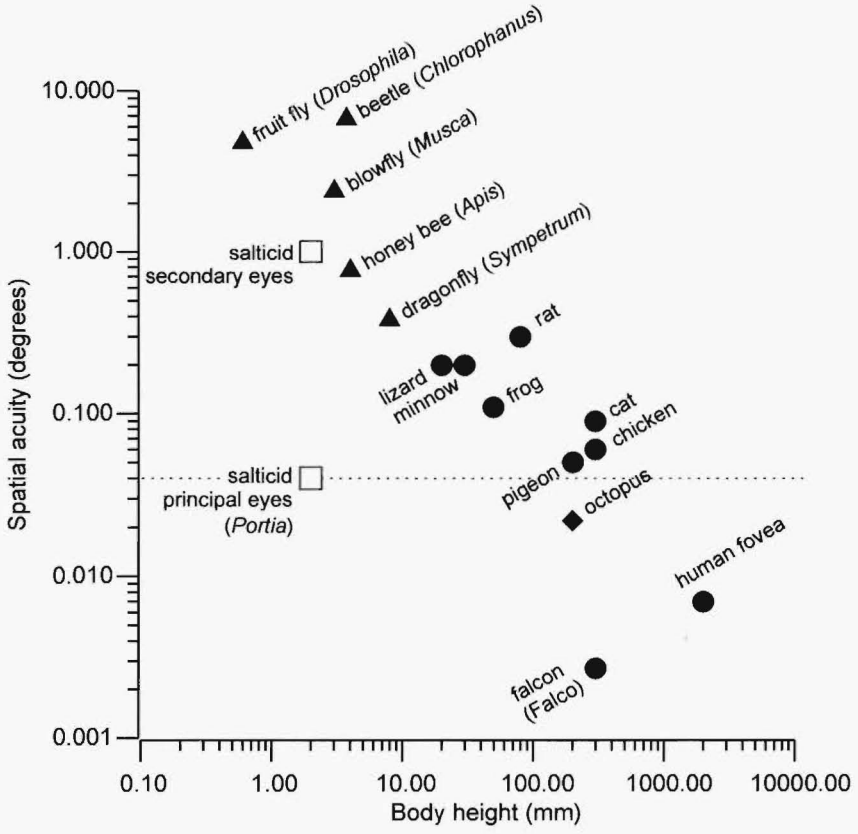

Figure 2. Spatial acuity of Portia's eyes compared with that of other animals. Spatial acuity (expressed approximately as minimum inter-receptor angle) plotted against body height (logarithmic scale on both axes). Triangles: insect compound eyes. Squares: salticid eyes. Circles: vertebrate eyes. Diamond = cephalopod eyes. Modified after Kirschfeld (1976). Data from Kirschfeld (1976), Land (1985, 1997) and Snyder & Miller (1978).

Portia uses aggressive mimicry against, and catches, just about every kind of web-building spider imaginable, as long as it is in a size range of from about 1/10th to 2X *Portia*'s size (Jackson & Hallas 1986). Being able to make so many different kinds of signals is an important because how *Portia*'s prey, another spider, interprets web signals may vary considerably depending on the species to which it belongs, and its sex, age, previous experience and feeding state.

However, an ability to make so many different signals raises the next question. How does *Portia* derive the appropriate signals for each of its many victims from its enormous repertoire? Two basic methods appear to be critical (Wilcox & Jackson 1998): 1) using specific genetically pre-programmed signals when cues from some of its more common prey species are detected; and 2) flexible adjustment of signals in response to feedback from the prey (i.e., trial-and-error derivation of appropriate signals). The first, using pre-programmed signals, is consistent with the popular portrayal of spiders as animals governed by instinct, but trial and error is an example of problem-solving behaviour and less expected in a spider.

How *Portia* uses the trial-and-error tactic may be most easily appreciated when *Portia* enters the web of a species of web-building spider for which it does not have a pre-programmed tactic. After presenting the resident spider with a kaleidoscope of different web signals, *Portia* eventually chances upon a signal that elicits an appropriate response from the victim, whereupon *Portia* ceases to vary its signals and concentrates instead on producing this particular signal (i.e., the signal that worked; Jackson & Wilcox 1993a). When *Portia* is larger than its intended victim interpreting the predatory sequence appears to be straight forward: *Portia* homes in on signals that cause the resident spider to approach as though *Portia* were a small ensnared insect (Jackson & Blest 1982; Tarsitano

et. al, in press). However, the function of signals often may be more subtle than this.

In encounters with a large and powerful spider in a web, simply mimicking a trapped prey and provoking a full-scale predatory attack would be highly dangerous, and *Portia* appears adopt an alternate goal: fine control over the prey's behaviour (Jackson & Wilcox 1998). *Portia* may make signals that draw the prey spider in slowly, or *Portia* may pacify the prey with monotonous repetition of a habituating signal while moving in slowly for the kill.

Trial-and-error derivation of signals may enable *Portia* to manoeuvre a prey spider into a particular orientation before attacking. Pholcids, for instance, are especially dangerous spiders. They have very long legs and, once a leg is contacted, pholcids defend themselves and sometimes kill *Portia* (Jackson 1990, 1992a, 1992b). The best way for *Portia* to catch a pholcid is to grab hold of its body without first hitting a leg. Using trial-and-error signal derivation, *Portia* may coax the pholcid into a position from which a clear shot at the body is possible.

Even during encounters with spiders for which *Portia* has pre-programmed signals, trial and error may still be relevant, as the role of the pre-programmed signal to initiate the predatory sequence in an optimal fashion, after which adjustments are made by using trial-and-error signal derivation (Jackson & Wilcox 1998). The victim spider may, for instance, start to approach slowly, then lose interest, become distracted, or begin approaching too fast. When, for any reason, pre-programmed signals fail, *Portia* switches to trial-and-error signal derivation.

Flexibility in *Portia*'s predatory strategy is a factor not only when generating signals, but also during navigation, with detouring behaviour being the most extensively studied example of this (Tarsitano & Andrew 1999). *Portia* routinely reaches prey by taking indirect routes (detours) when direct paths are unavailable (Tarsitano & Jackson 1993), including 'reverse-route detours' (i.e., detours that require movement initially away from prey) (Tarsitano & Jackson 1994,1997). In

encounters with some of its prey, *Portia* takes detours even when direct routes are available (Jackson & Wilcox 1993b). For example, *Scytodes* sp., a spitting spider from the Philippines is particularly dangerous because its preferred prey are salticids (Li *et al.* 1999). By taking detours, Philippines *Portia* approach spitting spiders from the rear, the safer end (Jackson *et al.* 1998).

That *Portia* makes pre-planned detours been corroborated in laboratory experiments. For example, when allowed to choose between two routes on artificial vegetation in the laboratory, only one of which leads to a prey spider, *Portia* consistently takes the appropriate path even when this means initially going away from the prey, going to where the prey is temporarily out of view and going past where the inappropriate path begins (Tarsitano & Jackson 1997). Lions have been observed making comparable detours when hunting their prey (Schaller 1972). The taking of detours by lions, although not studied experimentally, has also been interpreted as demonstrating planning ahead. Lions, however, are much bigger animals with much bigger brains, and they are mammals.

Salticids may have comparatively larger brains than other spiders (Meyer *et al.* 1984), but the salticid brain is still minute when compared to the much larger brains of mammals. We might envisage a brain as something more or less like a computer, and common sense tells us that a complex computer needs a lot of components. Miniaturising a computer requires miniaturised components, but miniature animals, such as spiders, do not have miniaturised neurons. As a rule, smaller animals simply have fewer neurons (Alloway 1972; Menzel *et al.* 1984), and an elementary engineering problem would seem to work against animals in the salticid's size range. With so few components, how can they orchestrate complex and flexible behaviour?

One of our long-term objectives has been to clarify how *Portia*, despite operating with a miniature nervous system, adopts a predatory strategy that rivals a lion's. *Portia*'s acute eyesight raises a parallel question: how can *Portia*, a spider with eyes that are minute compared with the

eyes of a cat or a person, see so well? Understanding how salticid eyes work is currently more tractable than understanding how salticid brains work, but the kinds of answers that apply to small eyes may also apply to small brains.

How well does *Portia* see?

In *Portia*, complex behaviour and acute vision are tightly interrelated. For example, planning and executing detours is based primarily on seeing features of the environment (Tarsitano & Andrew 1999) and *Portia*'s complex, flexible prey-capture tactics rely on using optical cues for resolving the identity and behaviour of prey from a distance (Jackson 1995; Li & Jackson 1996; Li *et al.* 1997). For example, recent work has shown that *Portia* can readily distinguish between an insect and a spider, regardless of whether the two prey are in or out of webs, but finer distinctions are made as well between different types of spiders (and different types of webs) against which species-specific prey-capture tactics are deployed. *Portia* can also distinguish between egg-carrying and eggless spiders, and the orientation of the spider. For example, *Portia* tends to approach eggless spitting spiders from the rear, whereas egg-carrying spitting spiders are approached head on.

Good eyesight might mean a variety of things, but it is perception of shape and form that is especially relevant for understanding *Portia*'s predatory strategy. Seeing shape and form depend critically on an eye's spatial acuity. Comparing *Portia* with insects, there is no known rival. *Sympetrum striolatus,* a dragonfly, has the highest acuity (0.4°) known for insects (Labhart & Nielsson 1995; Land 1997). The acuity of *Portia*'s much smaller eyes is 0.04° (Williams & McIntyre 1980), exceeding that of the dragonfly by tenfold. Yet the compound eyes of the dragonfly are comparable in size to *Portia*'s entire cephalothroax. The human eye, with acuity of

0.007° (see Land 1981), is only five times better than *Portia*'s. In practical terms, acuity of 0.04° means that *Portia* may be able to discriminate, at a distance of 200 mm, between objects spaced no more than 0.12 mm apart. Spatial acuity of other salticid eyes tend not to be far behind that of *Portia* (Harland *et al.* 1999; Jackson & Blest 1982b).

Explaining how *Portia* can see with acuity more similar to that of a mammal rather than that of an insect (Fig. 2) is not a trivial problem. The size difference is enormous. There are more than 150 million photocells in the human retina, but the photocells in a salticid's eyes number only in the thousands (Land 1969a).

The design of salticid eyes

Salticids have eight eyes (Fig. 3). Six of these, the secondary eyes, are positioned along the sides of the carapace and function primarily as movement detectors (Land 1971). However, it is a pair of large forward-facing antero-medial eyes (called the 'principal eyes') that give salticids their catlike appearance, and these eyes are responsible for acute vision.

Compound eyes, as found in most insects, are absent in spiders. Spiders have what are known as 'camera eyes'. Mammals also have 'camera eyes', but salticids' principal eyes are, in their details, very different from the camera eyes of mammals or any other animals. Many of these details appear to be solutions to the problem of accommodating a high-resolution eye in a small body, as neither compound eyes nor spherical humanlike eyes would seem to be feasible for a spider. Compound eyes with acuities approaching those of *Portia*'s principal eyes would not be supportable on a body of *Portia*'s size, and there is insufficient space inside *Portia*'s body for humanlike spherical camera eyes of equivalent acuity (Land 1974).

What we know about the structure of the principal eye and the function of its components

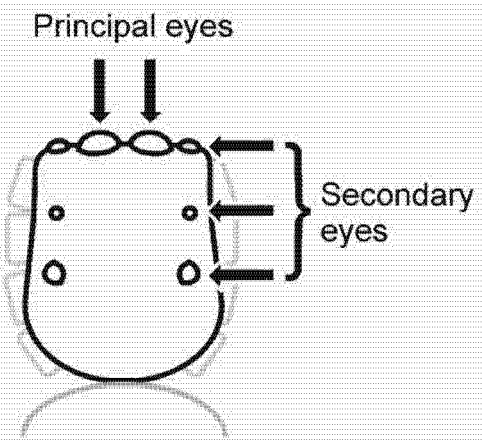

Figure 3. Salticid eyes. Secondary eyes alert salticid to nearby movement. Principal eyes, with high spatial acuity, allow salticid to detect fine details and identify distant objects.

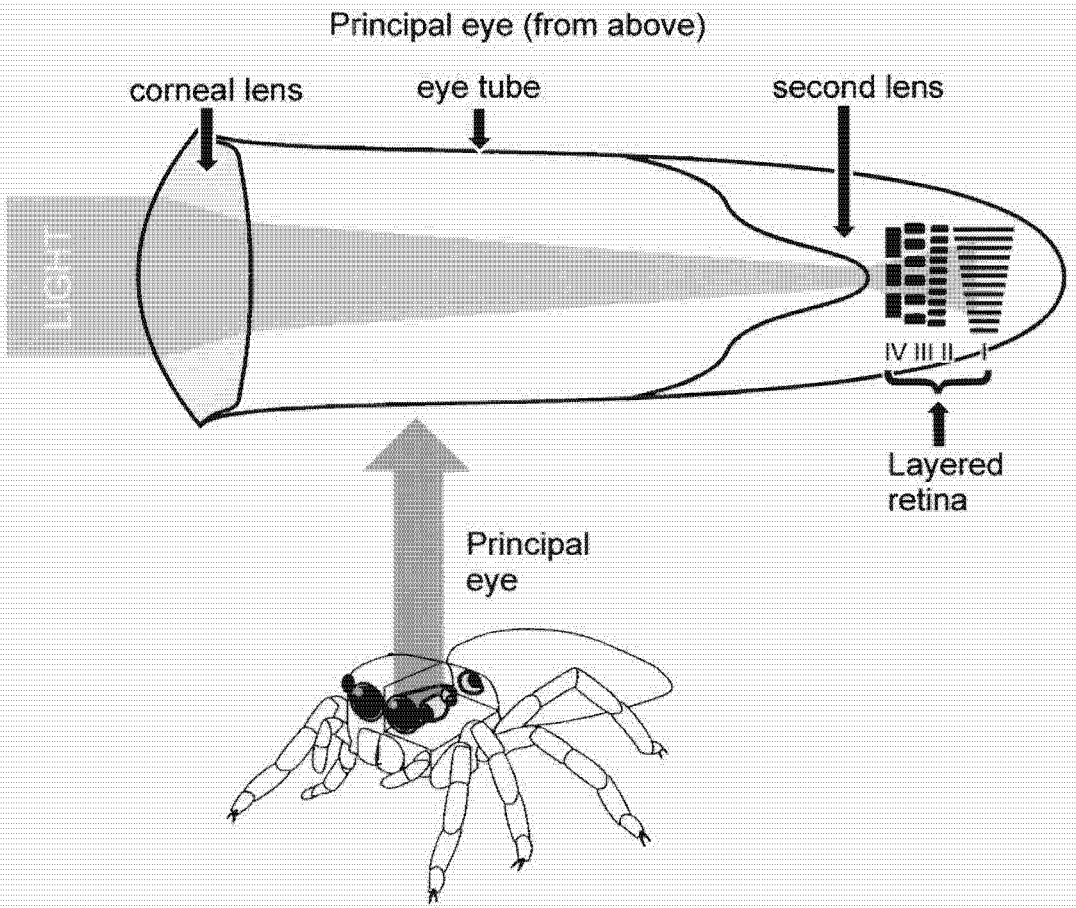

Figure 4. Internal structure of the salticid principal eye. Below: position of eye in cephalothorax. Above: light passes through a corneal lens and down an eye tube where it is magnified by a second lens before falling onto a four-layered retina. Layers II-IV function in colour vision. Layer I functions in high-acuity perception of shape and form.

can be illustrated by following the path taken by light passing into the eye. On the outside are the two large corneal lenses. These lenses have long focal lengths (i.e., they are good at magnifying distant objects). Having binocular overlap, the combined field of view of the two corneal lenses covers an ambit of roughly 90° in front of the salticid. However, a retina that could sample this whole field at once with the kind of acuity implied by salticid behaviour would have to be so large that it could not begin to fit inside the salticid's principal eye. The solution is surprising. There is a long, narrow eye tube behind each corneal lens, with a small retina at the end (Fig. 4). The retina's horizontal field of view is only 2-5° (Land 1969b), much less than the 90° taken in by the corneal lenses.

On the basis of appearance this pair of corneal lenses and pair of long eye tubes resembles a pair of binoculars. This resemblance is more than superficial. Just before reaching the retina, light passing down the eye tube encounters a second lens (a concave pit) that augments the magnification of the corneal lens. This means that the salticid principal eye is a telephoto system because the corneal lens has a long focal length and a second lens at the rear of the eye tube magnifies the image from the corneal lens (Williams & McIntyre 1980).

Light imaged through the telephoto-lens system comes into focus on a complex retina. The human retina is arranged in a single plane, but the salticid receives light successively on four layers of receptors, stacked along the light path. This tiered arrangement functions critically in colour vision (Land 1969a). Light entering each principal eye is split into different colours (chromatic aberration) by the corneal and secondary lenses. Different wavelengths (colours) of light come into focus at different distances, and these distances correspond to the positions of different layers in the retina. Using this system, salticids discern green, blue and ultraviolet (Blest *et al.* 1981).

For understanding perception of shape and form, it is the rearmost layer (i.e., the green layer; called 'layer I') that matters because only here are receptors spaced close enough together to support high-acuity vision (Blest *et al.* 1990). There is a central region of layer I, called the 'fovea', where receptors are especially close together (inter-receptor spacing of about 1 micron). Spacing at 1 micron seems to be optimal. The telephoto optical system is precise enough to let the retina sample at this resolution, but spacing any closer than this would reduce the ability of the retina to sample the image because of quantum-level interference between adjacent receptors (Blest & Price 1984; Williams & McIntyre 1980).

Two factors critically influence the acuity of an eye, the quality of the receptor mosaic and the quality of the image (Land 1981). One problem with maintaining a good image quality is that objects at different distances in front of the eye come into focus at different distances behind the lens. This means that, when a close object is in focus, a more distant object is likely to be out of focus. Ability to accommodate (by changing the shape of the lens) solves this problem in our own eyes, but this is not the solution adopted by salticids. Unlike our own eyes, or a pair of binoculars, the salticid principal eye cannot be focussed. Instead, a clever arrangement of the layer-I receptors makes focal adjustments unnecessary. Different parts of layer I are positioned on a 'staircase' at different distances from the lens. This means for any object, whether only a few centimetres or many metres in front of the eye, will cast an in-focus image on some part of the layer-I staircase (Blest *et al.* 1981). Another surprising feature of the salticid principal eyes makes this solution work. The eye tubes can swing side to side while the corneal lenses remain static. This means that the salticid can sweep the staircase of each retina across the image generated by the corneal lens. However, eye-tube movement may have significance that goes beyond solving the focussing problem.

The human eye and the salticid principal eye are similar in that a high-acuity central region (a fovea) is used for resolving fine detail, but there is a major difference in scale. The fovea in each of *Portia*'s principal eyes has a field of view only 0.6 degrees wide and contains only a few hundred receptors, yet *Portia* somehow uses this miniature system for routinely making the fine-scale distinctions necessary to sustain its complex vision-guided behaviour. How this is achieved is not fully understood, but eye-tube movement may be the key.

Six muscles attached to the outside of each principal eye tube allow the same three degrees of freedom (horizontal, vertical, and rotation) as in each of our own eyes (Land 1969b). Using these muscles, the salticid sweeps the two eyes' fields of view in complex patterns over the scene coming into the eye from the telephoto lens system.

Eye-tube movement enables the salticid to sample from the larger image projected by the corneal lens, and patterns of movement can be complex. This suggests that eye-tube movement patterns are intimately involved in how salticids process visual information, serving as critical steps in the perception of shape and form (Land 1969b). One intriguing possibility is that, by using specific patterns of eye-tube movement, a salticid may search images for particular pieces needed for arriving at perception of specific objects.

Portia's limitations

Extensive sampling may be the salticid's answer to the problem of how to see details of shape and form within the constraints imposed by small size, but speed may be a primary limitation. From many years of studying *Portia*, our impression is that, although these spiders' feats of discrimination are impressive, they are often strikingly slow on the uptake. It may be that *Portia* can see more or less what we can see, but achieves this by means of a slow scanning process. Part

of what it means to say an animal 'sees well' should perhaps be that it perceives what is out there quickly. On this criterion, *Portia* may see only poorly.

Another potential limitation is that the small size of *Portia*'s fovea may limit perception of large objects. Images of small features of animals (e.g., a palp, leg or eye of a spider) may be more or less easily sampled by the salticid fovea, whereas sampling critical body parts of larger animals may be exceedingly difficult. When *Portia* scans with its foveas across smaller objects, such as its usual spider prey, piecing together a 'picture' of what it is looking at may be much more feasible than when scanning in a 'picture' of a larger animal such as a bird, a frog or a large mantis, all of which are relevant to *Portia*. Mantises, for instance, readily prey on *Portia*, yet *Portia* typically shows no evidence of taking appropriate precautions when coming face to face with these deadly foes. Our impression is that *Portia* often looks at large mantises and then fails to discern what they are.

When it comes to seeing, it seems that *Portia* has made efficient use of its limited materials and overcome many, but not all, of the limitations imposed by small size. The same basic principle may apply to cognition. It may be that by making efficient use of limited brain resources (neurons), *Portia* can achieve considerable cognitive skills, such as problem solving and planning ahead, all the while suffering limitations comparable to those that apply to seeing. For example a big difference between *Portia* and cats may be the speed at which problems are solved.

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Appendix B. Reading a Spider's Mind

By Robert R. Jackson & Duane P. Harland

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Reading a Spider's Mind

Good vision, flexible problem solving, deception and manipulation — who can fathom the mind of a spider?

Robert R. Jackson
and Duane P. Harland

Unique eyes, acute vision and complex behaviour are the distinctive features that separate the jumping spiders (of the family Salticidae) from all other spider families. Salticids enjoy a visual acuity approaching that of humans and exceeding that of any other animal of comparable size. One of our objectives has been to investigate the interrelationship between acute vision and complex behaviour in these unique animals.

We have been especially interested in *Portia*, a genus of salticids with exceptionally complex behaviour and perhaps the most acute eyesight of any salticid. The resolving power of *Portia*'s eyes is about two minutes of arc, or six times greater than the highest acuity known for insects (found in a large dragonfly with compound eyes roughly equal in size to *Portia*'s entire body) and is only six times less than that of humans. Although a spider is not a conventional subject of cognition studies, we have been investigating how *Portia*'s eyes work as part of a broader interest in animal cognition.

Most salticids eat insects captured in the open without using a web, but *Portia* is an oddball that routinely enters the webs of other spiders to catch and eat the resident. Hunting in the prey spider's own web is dangerous, but *Portia* avoids becoming its intended dinner's own dinner by using complex, flexible behaviour to deceive and manipulate its victim.

The web spiders on which *Portia* preys, having poor eyesight, perceive the world around them primarily by interpreting web signals. Web signals are the tension, movement and vibration patterns transmitted across the silk comprising the web — the spider's web can be envisaged as not only a snare for catching prey but also a component of the web spider's sensory apparatus.

Portia's success at araneophagy (or spider-eating) depends largely on being able to orchestrate the pattern of web signals received by the resident spider, a predatory tactic we call "aggressive mimicry". Using any combinations of its eight legs and two palps, *Portia* can produce a virtually unlimited array of web signals to control the behaviour of the resident spider prior to the attack [What is that Spider Thinking, Feb 95].

Portia's different prey spiders tend to be responsive to different signals, but *Portia* finds the appropriate signals by using a dynamic blend of pre-programmed tactics and trial-and-error derivation of signals. Trial and error is based on *Portia* using feedback from the prey spider to adjust the characteristics of the signals. Such flexible problem solving is perhaps surprising in a spider.

As another example of flexible problem solving, *Portia* routinely makes detours when it pursues prey. For instance, *Portia* may take a path to reach a particularly dangerous spider from behind. We know from experiments that many of *Portia*'s detours are planned ahead of time on the basis of preliminary viewing of the environment. Planned detours depend on acute vision. In fact, excellent eyesight is critical to much of the complex, almost mammal-like behaviour that makes *Portia* so fascinating.

Excellent Eyes

Salticids have eight eyes, but it is the large, forward-facing antero-medial eyes (principal eyes) that are responsible for acute vision. The other secondary eyes are primarily movement detectors. The principal eyes of salticids are very different from the multi-faceted compound eyes of insects. Instead, the salticid eye, like our own, has a single lens and a single retina. However, the way in which the salticid principal eye works differs from how a vertebrate eye works.

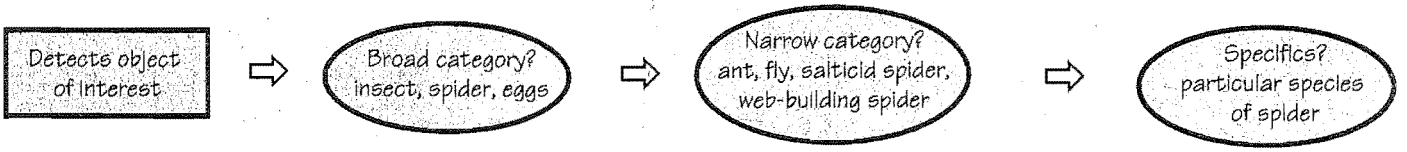
The salticid principal eye has a static corneal lens fixed to the carapace at the front of a long eye tube. In contrast, our own eyes are spherical with a corneal lens that moves with the rest of the eye and can be flexed during focussing. Unlike our own eyes, the salticid principal eye cannot accommodate — it can not change focal length. Space is so limited in the salticid's small body, that lengthening the eye tube to focus is not feasible.

The principal eye is a telephoto system as a consequence of the eye tube being long and because there is a second lens at the back of the eye tube which magnifies the image from the corneal lens, turning this eye into a miniature telescope.

Within the salticid principal eye retina, photoreceptors are stacked in four layers at the rear of the eye tube, whereas our rod and cone photore-

Mirroring a Spider's Mind

A recent model of Portia's decision process, which is more complex than the traditional model but still too simplistic. The circles represent decisions; rectangles are responses.



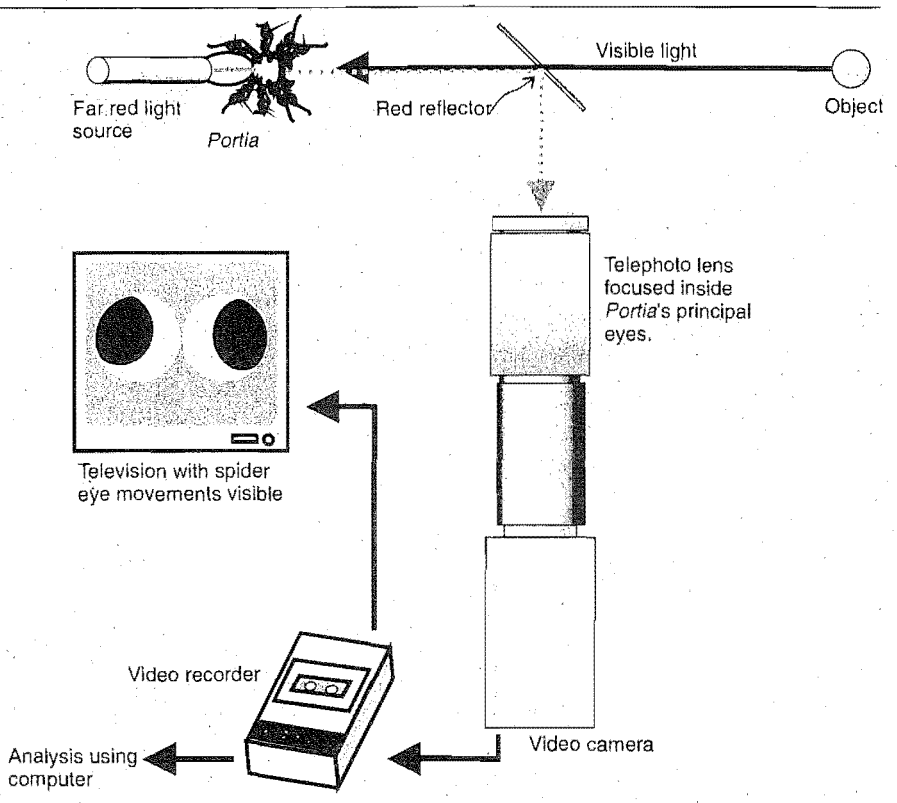
ceptors are on one plane. The centre of the back-most layer is a fovea, a fine-grain, regular mosaic of receptor cells where small inter-receptor angles maximise acuity. This fovea contains only a few hundred receptors, and the field of view covered by the fovea is only a small part (about 2°) of the field covered by the corneal lenses of the principal eyes (about 25°). Six muscles attached to the outside of the eye tube allow the salticid to sweep the fovea's field of view over the scene coming through the fixed corneal lens.

Our knowledge of salticid eyes comes especially from the groundbreaking research by Michael Land of Sussex University, England, carried out 30 years ago, and more recent work by David Blest at Australian National University. Land suggested that the intricacy of the eye-tube movement may be part of the mechanism by which the salticid perceives shape and form, but precisely how this might be achieved is poorly understood.

One exciting possibility is that the salticid, by adopting particular patterns of eye-tube movement, may be searching for specific identifying features of the object being viewed. The behaviour of the salticid's eyes may reveal how perception is achieved. Yet 30 years later, Land's pioneering study is still almost everything we know about salticid eye-tube movement. Methodological difficulties, including the need for a specialised opthalmoscope, have probably discouraged further research.

Recently, we devised a system for studying how eye-tube movement may function in the processing of optical cues, and one of us has built a prototype opthalmoscope based on Land's design. Our goal is to record pattern of eye-tube movement while *Portia* views the objects we place in its field of view during experiments.

Our goal is to go beyond studying reception, a term for when an animal takes in raw information from the sense organs. We are also interested in representation, a term for a cognitive level one step beyond reception. This term refers to the moulding of raw sensory input into what is needed for identifying objects and solving problems.



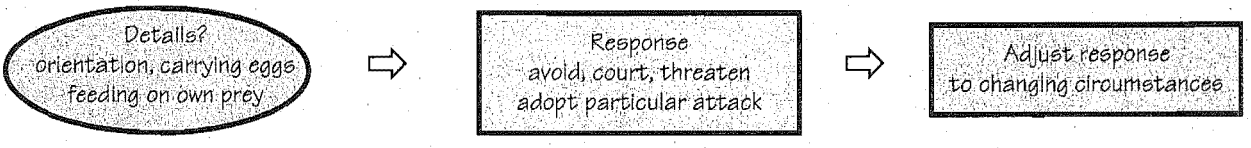
The apparatus used to study salticid eye-tube movement. The spider is given an object to look at. Red light, which is invisible to the salticid, is used to illuminate the eye tubes and observe their movement.

The conventional wisdom used to be that representation in salticids is based on the use of only a few simple optical cues to discriminate between objects belonging to only a few broad categories. In reality, the model implied is probably far too simplistic for any salticid, and representation is certainly much more complex than this in *Portia*. This is illustrated by examples from recent work on the things *Portia* can distinguish:

- insects from spiders, regardless of whether the two prey are in or out of webs
- flies (on which *Portia* preys) and ants (which *Portia* avoids)
- different species of spiders
- the spider and the spider's eggs
- spiders that are feeding on their own prey (insects) and spiders that are not feeding
- the orientation of the spider (whether it is facing forward or away)

It is *Portia*'s large repertoire of distinct behavioural responses that enables us to ascertain when discriminations are made, because in each instance performance of a different behavioural sequence provides the objective evidence that *Portia* has made a discrimination. Movement of the object is unnecessary for any of these discriminations, chemical cues are ruled out by the experimental design and, in general, shape and form alone appear to be sufficient. A more complex model has been suggested, but even this is almost surely too simplistic.

We are currently investigating the optical cues by which *Portia* makes these and other discriminations. Experimental protocol includes presenting *Portia* with models made from dead spiders and insects that we mount in lifelike postures on small pieces of cork. Features of the models



are altered systematically. For example, we alter the size of the eyes and the length and orientation of the legs. Also, one of us has also developed a system for testing *Portia* with virtual objects generated by computer 3-D animation and displayed to *Portia* through a high resolution projector. Using this system, which is a first of its kind for studies of salticid vision, we can achieve very precise control over the optical cues given to *Portia*.

Some preliminary findings have been intriguing.

Most spiders have eight eyes, but salticids are unique because their two antero-medial eyes are much larger than the other six. This is an important taxonomic character for distinguishing salticids form other spiders. Our findings indicate that *Portia*, like the human taxonomist, relies on the relative size of the spider's antero-medial eyes when distinguishing salticids from other spiders.

Portia is itself a salticid, yet *Portia* responds differently depending on whether the salticid it encounters is or is not another *Portia*. Important cues include distinctive tufts of hair on *Portia*'s legs which are absent from the legs of more typical salticids.

Pholcids, web-building spiders with especially long legs, are common prey of *Portia*. When *Portia* contacts a pholcid's leg, it often gets wrapped up and eaten. *Portia* compensates by being especially careful to achieve an orientation from which the pholcid's body can be attacked without contacting a leg. Important cues for recognising a pholcid include presence of legs that are at least five times longer than the body.

About 50 years ago, Keith McKeown, an Australian naturalist, asked rhetorically, "Who can fathom the mind of a spider?" When we first began to study spider behaviour, McKeown's question struck us as almost comical. Our attitude has changed over the years, and we are now taking seriously questions about spider cognition. Perhaps, no one will ever fully fathom the mind of a spider, but the question no longer appears so foolish as we might first have thought.

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